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VOL
27
194

STOCKHOLM. ALB. BONNIERS BOKTRYCKERI 1947

# INNEHÅLL


NILS HOLMGREN: On Two Embryos of Myxine glutinosa . . . . . 1

PER ERIC LINDAHL: On Some Archaic Features in the Developing Central Stem of the Mammalian Chondrocranium . . . . . 91

PER ERIC LINDAHL and MAJ LUNDBERG: On the Arteries in the Head of Procavia capensis Pall. and Their Development . . . . . 101

V. L. WAGIN: Ascothorax ophioctenis and the Position of Ascothoracida Wagin in the System of the Entomostraca . . . . . 155



OL.
27
946

# ASCOTHORAX OPHIOCTENIS AND THE POSITION OF ASCOTHORACIDA WAGIN IN THE SYSTEM OF THE ENTOMOSTRACA

BY

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VOL. 27 194

CONTENTS.

I. Introduction . . . . . 156
II. Historical survey . . . . . 157
III. Material and method of investigation . . . . . 161
IV. Description of Ascothorax ophioctenis . . . . . 162
A. The external anatomy, segmentation and size . . . . . 162
a) The shape and size of the body . . . . . 162
b) Pigmentation. The colour of the body . . . . . 165
c) The mantle . . . . . 165
d) The segmented body . . . . . 167
e) The cephalic appendages . . . . . 169
1) The antennules . . . . . 169
2) The oral pyramide . . . . . 172
f) The appendages of the thoracic portion . . . . . 174
B. The internal anatomy . . . . . 176
a) The integument . . . . . 176
b) The nervous system and organs of sense . . . . . 176
c) The gut . . . . . 179
d) The muscles of the body proper . . . . . 184
e) The connective tissue . . . . . 187
f) The lacunary system . . . . . 188
g) The excretory system . . . . . 188
h) The reproductive system . . . . . 189
i) An unknown glandular organ in females . . . . . 191
C. Development . . . . . 192
a) The fertilization and the laying of the eggs . . . . . 192
b) The nauplius . . . . . 193
c) The metanauplius . . . . . 194
d) The ascothoracid stage . . . . . 194
D. The relation of parasite to host . . . . . 200

V. Comparative survey of the Ascothoracida . . . . . 206
A. The body form, segmentation and appendages . . . . . 206
a) The bodyform and the mantle . . . . . 207
b) The segmented body . . . . . 209
B. The appendages . . . . . 210
a) The antennules . . . . . 210
b) The antennae . . . . . 215
c) The oral apparatus . . . . . 216
d) The appendages of the thoracic portion . . . . . 218
C. Anatomy . . . . . 220
a) The integument . . . . . 220
b) The nervous system and the organ of sense . . . . . 221
c) The alimentary system . . . . . 222
d) The muscles of the body . . . . . 224
e) The connective tissue and the lacunary system . . . . . 225
f) The excretory system . . . . . 225
g) The reproductive system . . . . . 226
h) Fertilization . . . . . 230
D. The larvae . . . . . 230
a) The Nauplius stage . . . . . 231
b) The Ascothoracid larvae . . . . . 232
E. The relation of parasite to host . . . . . 233
F. The relation between the sexes . . . . . 236
G. Geographical distribution . . . . . 239
H. The phylogeny of the Ascothoracida . . . . . 240
I. The position of Ascothorax ophioctenis in the system of Ascothoracida . . 245
VI. The position of the Ascothoracida in the system of Entomostraca . . . . . 246
A. A comparison with the Cirripedia . . . . . 246
B. A comparison with the Copepoda . . . . . 253
C. The position in the system . . . . . 260
VII. Summary . . . . . 262
Literature cited . . . . . 264

OL.
27
946

VOL
27
194

# ON TWO EMBRYOS OF MYXINE GLUTINOSA

BY

*NILS HOLMGREN*

VOL. 27 1946

CONTENTS


1. Introduction . . . . . 2
2. The "abortive" eggs . . . . . 6
3. The two *Myxine* embryos . . . . . 7
4. The head . . . . . 10
5. The skull of the adult *Myxine* . . . . . 13
6. The skull of the embryo . . . . . 15
   A. The basis cranii and the auditory capsules . . . . . 15
      The notochord . . . . . 15
      The parachordals and the basiotic lamina . . . . . 16
      The trabeculae . . . . . 18
   B. The nasal capsule and duct . . . . . 20
   C. The visceral skeleton . . . . . 22
7. Some points of relations between the cranial nerves and the visceral skeleton . 27
8. Interpretation of the Myxinoid skull . . . . . 29
9. The muscle rudiments of the head of the embryo . . . . . 34
10. The skin . . . . . 38
11. The brain . . . . . 41
   A. Lateral aspect . . . . . 42
   B. Dorsal aspect . . . . . 43
   C. Ventral aspect . . . . . 44
   D. The sagittal section . . . . . 45
   E. The ventricular wall . . . . . 47
      The telencephalon . . . . . 47
      The diencephalon . . . . . 48
      The mesencephalon and the cerebellum . . . . . 52
      The medulla oblongata, the nerve roots and the cephalic ganglia . . . . . 54
      The spinal chord . . . . . 56
12. The vascular system . . . . . 57
   A. The arterial system . . . . . 57
      Branchial part . . . . . 57
      Phylogenetical considerations . . . . . 65
      The "prebranchial" part . . . . . 67
   B. The venous system . . . . . 70
   C. The venous system of the adult *Myxine* and of the embryo . . . . . 74
13. The body cavity . . . . . 76
14. The alimentary canal and the liver . . . . . 77
15. The pronephros . . . . . 80
Literature cited . . . . . 85
Explanation of letterings . . . . . 88
Acknowledgement . . . . . 90

## 1. INTRODUCTION.

Eggs of *Myxine glutinosa* provided with their characteristic anchor filaments have been recorded but a few times since they were first described by THOMPSON (1859). "Ripe" eggs were then mentioned or described by STEENSTRUP (1863), CUNNINGHAM[1] (1886), RETZIUS (1888) and KLINCKOWSTRÖM (1895)[2]. The number of fully developed eggs found *deposited* does not seem to have been very large. Records in literature are mentioned by BASHFORD DEAN (1899). W. MÜLLER (1875) obtained two fertilized eggs from the Gothenburg Museum (doctor A. W. Malm). They were attached to one another through their filaments. NANSEN (1887) records one egg in 1857 dredged by DANIELSSEN at Molde, in Norway, and J. HJORT and K. DAHL (1900) found no less than 23 eggs in the Dröbak fiord. These eggs were mostly aggregated in clusters or bunches, each containing 3 to 13 eggs. They were caught in shrimp trawls from a depth varying from 50 to 60 fathoms on an oozy bottom. The biggest cluster was illustrated.

From this time on I have found no records of naturally deposited eggs of *Myxine*. Meanwhile single eggs have been taken on the Swedish west coast. At the Kristineberg zoological station eggs have been brought in occasionally. Most of these eggs have been caught in shrimp-trawls, always from an oozy bottom. At the zoological station doctor G. GUSTAFSON has succeeded in keeping *Myxine* alive in aquaria for lengthy periods. The animals have even deposited single eggs. As, however, no males were available, the eggs were unfertilized and thus did not develop.

As mentioned in the preceding lines, the only "fertilized" eggs of *Myxine* hitherto recorded in literature are those described by W. MÜLLER (1875). W. MÜLLER says: "Nach Abzug der Eihäute zeigte sich an dem einen Eipol über dem Dotter eine annähernd kreisförmige etwa ¼ des Dotters umgebende Keimscheibe, welche bestimmte Embryonalanlagen noch nicht erkennen liess."[3]

Since 1924 I have made attempts to secure developmental stages of *Myxine*, making numerous dredgings with a specially constructed dredger, but always in vain. I did not get a single egg with the dredger. In 1924, however, I received from fishermen one egg collected in the fiord Gullmaren near Lysekil. It was

[1] The egg illustrated by CUNNINGHAM was probably the same as that of THOMPSON.

[2] The egg found by KLINCKOWSTRÖM was found in the eel-pot, used for catching the animals in, together with a large number of hagfish. The egg had probably been pressed out from a female and was thus probably not laid in the normal way.

[3] It may be observed that I have many times found poorly preserved eggs with patches of a light colour, suggesting the presence of an embryonic disc, but on closer investigation those eggs invariably were found to be unfertilized. NANSEN has stated that the eggs mentioned by W. MÜLLER were given to him by Dr. Malm at Gothenburg. MALM mentions them in his "Bohuslän fauna", as hawing been taken from the stomach of a cod. Therefore they must have been very poorly preserved, probably so poorly that an embryonic disc could not have been distinctly recognized.



VOL
27
194

VOL. 27 1946

taken in a shrimp trawl on an oozy bottom. This first egg was not followed by others until 1938, when I asked my friend dr. Orvar Nybelin, director of the Gothenburg Natural Museum, to tell me if there should occassionally be any eggs in the collections of the Museum. He then sent me 8 fully developed eggs taken by fishermen in Danish waters, some at Hanstholmen and the others at Koppargrund. Later he sent me 9 eggs from a depth of 200 metres northwest off Skagen and off Stora Pölsan. Dr Nybelin then was so very kind as to engage a number of fishermen to pick up any *Myxine* eggs which they occassionally got in their fishing nets. A liberal reward was promised for each egg, and bottles of Bouins fluid were distributed to the fishermen. Unfortunately their activities was interrupted by the war, but in the years 1939 to 1944 no less than 113 deposited eggs were obtained. They were collected at a depth of between 100—200 m off Hållö, Laesö, Skagen and Hirtshals. *All these eggs proved to be unfertilized,* as were all the others, with the exception of two; these contained developing embryos, which will be described in this paper. These two eggs were taken on two different occasions off Stora Pölsan near Marstrand.

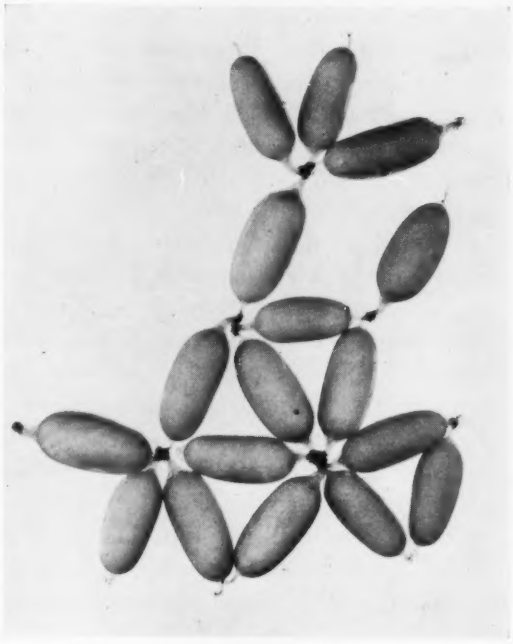

Fig. 1. Cluster of (17) abortive *Myxine* eggs. This cluster originally contained 21 eggs. It is "opened" and the eggs spread out in a single layer. Somewhat less than natural size.

Most of the eggs were taken during the summermonths June—August, but there were also eggs from March, April, May, September and October. Most of the eggs were found in small clusters of 5—6, but I have also obtained clusters (fig. 1) containing up to 21 eggs.[1] Single eggs or else eggs hooked together two and two are also present in my collection. The eggs are apparently laid throughout the year, as may be concluded from the development of the ovaries at different times of the year (Cfr. RETZIUS, CUNNINGHAM and others).

[1] The photographed cluster has been opened so that all eggs lie in the same level. In reality the eggs were so crowded, that scarcely a single tuft of bristles was free.

Under such circumstances the question arises: why are the fertilized eggs that have been taken so few: 2 out of 132, i.e. in two catches out of 28.

This wide disproportion between the number of fertilized and unfertilized eggs cannot be explained in any other way than that the two categories are deposited in different ways, the unfertilized being more accessible to the fishing tackle than the fertilized, i.e. the former being laid more or less superficially upon the oozy bottom, the latter being somehow buried in the bottom at such a depth that the tackle (shrimp-net, trawl) for the most part passed over the egg-level. Whereas the anchor filements of the unfertilized eggs were perfectly preserved, the anchors of the two fertilized eggs were all torn away. This must be due to the fact that these latter become fastened in some way in the mud so that they could not become detached without tearing the anchors. Unfortunately the circumstances attending the collecting of these two eggs are unknown, but it seems probable that the trawl dug down into the ooze sufficiently to reach the egg level. The possibility that the eggs were attached to stones, bryozoans, antozoans or other subjects is excluded, as the clusters are so constructed that nearly all the anchor filaments are attached to one another none being available for attachment to other subjects.

How, then can we explain the fact that the unfertilized eggs lie superficially, the fertilized ones being buried deep in the ooze? Different explanations seem possible.

1. The eggs are deposited superficially and then after fertilization are buried by the agency of the female or the male or both parents. If this were the case, one would expect to find at least some eggs with sperms in the micropyle canal or in an early stage of fertilization. It seems necessary therefore to believe that there was no male present when the female deposited her eggs. Then it is to be assumed that the male presented himself when the female was occupied with the act of the eggs burying or after the eggs had already been installed in their cave.

2. The superficially deposed eggs are abortive eggs, which probably were never destined to be fertilized owing to the absence of fertile males. The possibility of this hypothesis is supported by the fact that the fertile males, at least in certain localities, are very rare. If *Myxine* is a proterandric hermaphrodite — as alleged by CUNNINGHAM and NANSEN — this involves the fact that there must be a great predominance of females, as the male period of life is much shorter than the female. The number of fertile males or hermaphrodites with developed spermatozoa seems to be very variable in different localities. At the Firth of Forth CUNNINGHAM seems to have found but 3 individuals with developed spermatozoa, and he says: "In all the cases the number of spermatozoa was not large, and it is difficult to believe that fertilization is effected by such a meagre production of spermatozoa as was seen in the specimens I have mentioned. In no case have I discovered any



VOL
27
194

trace of spermatogenesis in a specimen which was completely masculine." (CUNNINGHAM's specimens were from January and March.) RETZIUS (1888) investigating the *Myxine* in the Gullmaren fiord on the Swedish West Coast (Kristineberg, Bohuslän), did not find any spermatozoa at all in about 840 specimens from different seasons, and after him no one has seen a single spermatozoan from *Myxine* of the Gullmaren fiord. At Bergen NANSEN (1887) found *Myxine* specimens with ripe or nearly ripe spermatozoa at every season of the year. Such specimens do not seem to have been particularly rare. At Dröbak SCHREINER (1904) also found a large number of such individuals, in which he studied the spermatogenesis.

The absence, or at any rate the rare occurrence, of fertile males in the Gullmaren fiord indicates that the *Myxine* does not propagate there or at least not to a degree corresponding to the abundance of hagfish in this water. (In a common eel-pot hundreds are captured in a few hours.) The unfertilized eggs occasionally found there must have been abortive eggs, like that described by KLINCKOWSTRÖM. Such abortive eggs could never be numerous as they are picked up by fishes such as cod and haddock, in which *Myxine* eggs have occasionally been found.

But even in waters where fertile males have been found in considerable numbers, as in the Dröbak fiord (SCHREINER, 1904) unfertilized *Myxine* eggs have also been found (HJORT and DAHL), a fact that seems to indicate that the number of fertile males has been too small for the much greater number of females.[1] In such waters females with fully developed eggs also seem to be extremely rare. These, then, are mysteries which cannot as yet be explained satisfactorily.

There are two possible explanations:

1. The ripe males and females lead a different life from the unripe, during oviposition perhaps buried so deep in the mud that they cannot be reached by our imperfect implements. During this period it must be supposed that they do not feed, otherwise they would be captured in the baited eel-pots like those hundreds of unripe animals which are captured in few hours. That the hagfishes do not eat often has been demonstrated by WORTHINGTON (1905) in respect of *Bdellostoma* and by GUSTAFSON (1934) in respect of *Myxine*. *Bdellostoma* did not display any exceptional hunger after a fast of seventeen days (WORTHINGTON) and *Myxine* can also stand a prolonged fast very well (GUSTAFSON). From this point of view there is thus nothing untenable in the preceding hypothesis, but it is refuted by the presence of the "abortive" eggs. This can, however, be explained by assuming that they are deposited by females which have not been able to find any ripe male and have therefore

[1] SCHREINER (1094) found at Dröbak 9991 distinct females and 353 distinct males in 1690 investigated specimens. The rest of the material consisted of hermaphrodites and sterile animals.

been forced to abortion, as they do when held in captivity (according to information obtained from Dr. GUSTAFSON). Against the above explanation is also the fact that ripe "male-hermaphroditic" or male specimens occur fairly abundantly at Bergen and Dröbak. It is not impossible, however, that these males had already fertilized a cluster of eggs and have now come to the surface of the ooze for feeding, or have not yet found any ripe female.

2. Another way of explaining the mysterious conditions is to assume a migration of the ripe or nearly ripe animals to especially favourable spawning beds. In the Gullmaren fiord most (all?) catches of *Myxine* recorded in literature have been made in relatively shallow water (40—45 m depth) near the mouth of the fiord, whereas catches in the inner, deeper (100 m and more) parts of the fiord have been undertaken only occasionally. Dr. GUSTAFSON at the zoological station of Kristineberg has told me that there may be a spawning bed in that part of the fiord and that females with nearly ripe or ripe eggs there are not particularly rare. Nevertheless no ripe males have been found there, nor any embryos. But from such a spawning bed the *Myxine* community of Gullmaren could very well get its supply of young specimens, which are very common also in the shallow parts of the fiord.

These two alternatives together may perhaps form the basis for an interpretation of the *Myxine* problem: The ripe specimens emigrate to spawning in the deep parts of the fiord, where the ripe females and males during oviposition live buried in the mud (or else under cover) without regularly coming to the mud surface for feeding.

## 2. THE ABORTIVE EGGS.

As it is possible that the unfertilized eggs which are found deposited are unripe or else abnormal in some way, I have subjected a number of such eggs to a special investigation on sections of their animal cap. This investigation has given the following results.

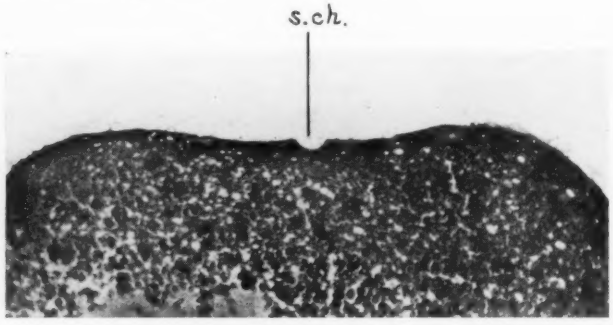


Fig. 2. Meridional section through the animal pole of an egg of *Myxine*.

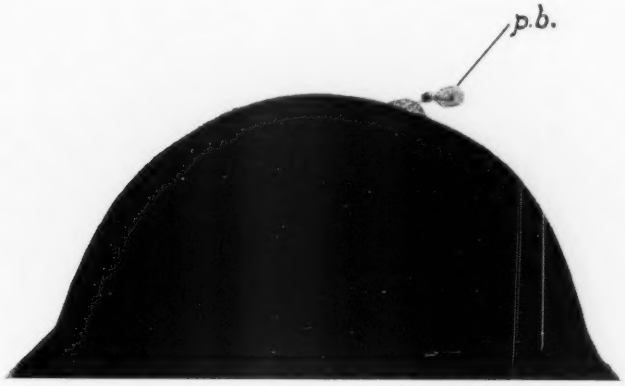


Fig. 3. Animal pole of an egg of *Myxine* with polar bodies.

VOL. 27 1946

1. On the surface of the anterior egg-pole there is a very distinct semihemisphaerical pit just inside the micropyle canal (Fig. 2). This pit is apparently intended to receive the spermatozoans entering through the micropyle canal and may be called a sperm-receptacle or micropyle-chamber.

2. The female nucleus always lies excentrically, never immediately below the micropyle, as has been assumed by previous authors. Thus the sperm must probably enter the egg from the sperm-receptacle at some distance from the nucleus.

3. The eggs, when deposited, have always been unripe, though displaying more or less advanced stages of ripening, the reduction division process being more or less advanced.

a) In some eggs the first polar spindle is present, the first polar body not yet causing any elevation on the surface of the egg.

b) Most eggs have already formed the first polar body. The polar body is for the most part somewhat sunk in the egg surface. In such eggs the second division is more or less advanced. In the diaster stage the second polar body is foreshadowed by an elevation on the surface of the egg.

c) In a cluster of eggs the second division was brought to an end and the first polar body was divided into two of different sizes. The reduced egg nucleus had already assumed a rounded shape. These eggs were apparently ripe, ready for fertilization. Such an egg is illustrated in fig. 3. The second polar body is sunk into the surface of the egg.

4. The "abortive" eggs are thus quite normal.

## 3. THE TWO *MYXINE* EMBRYOS

As already mentioned, I have obtained two eggs of *Myxine* containing embryos. As has also been mentioned, these eggs were devoid of the anchors

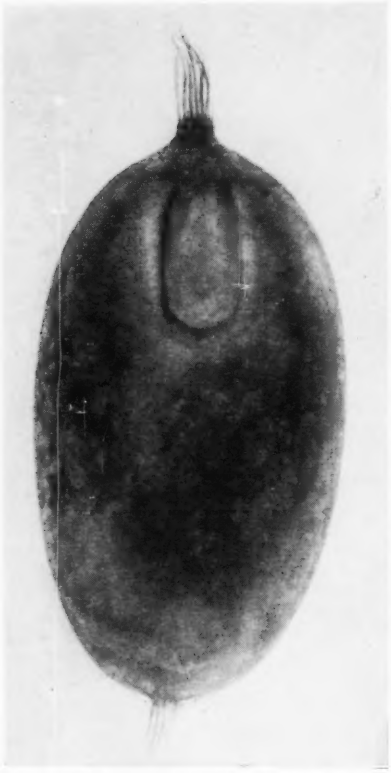

Fig. 4. The younger *Myxine* egg with embryo, ventral view.

at the ends of the filaments. Their shell was muddy, indicating that they were picked up out of mud collected in the fishing trawl. Otherwise I know nothing about the circumstances of their acquisition.

The state of preservation of the embryos is not very good as probably they were merely placed in alcohol. Nevertheless, the younger of the two is usable for anatomical purposes, whereas the older embryo is not so good, it having shrunk considerably. The sectioning of the older stage was not entirely successful, the yolk being a great hindrance. Of the younger stage, however, I obtained a rather good series of transversal sections 8 $\mu$ thick. From this series graphical reconstructions were made. The other series was chiefly used for comparative purposes.

Compared with *Bdellostoma* (DEAN, 1899) the eggs of *Myxine* are generally shorter. The unfertilized *Myxine* eggs have a width less than half their length (about 46 % of the total length), those of *Bdellostoma* are, according to DEAN, about three times as long as they are broad (average 34 %). In the two *Myxine* eggs containing embryos (fig. 4) the proportions are different, the breadth of the egg there being about 57 % of the lenght. I ascribe this difference in proportions to the pressure of the developing embryo.

The embryos represent two somewhat different stages. In both cases the cranial end of the embryo bends over the anterior pole of the egg (figs 5, 6). In the younger embryo the bent-over part extends caudad over the anterior third, in the older one it extends over about $^2/_5$ of the ventral surface of the egg. In the younger embryo the caudal end of the embryo lies at the posterior pole, in the older one it reaches the ventral surface of the egg.

DEAN (1899) has given a series of pictures of the different stages of the embryonic development of *Bdellostoma*. These pictures show very close agreement with those of my embryos. The outlines of the head portion of the embryo do not differ perceptibly in the two genera, though in the body portion there are differences.

My younger stage corresponds with that of *Bdellostoma* depicted by DEAN



VOL
27
194

in figs 51 or 53 in the extension of the head region upon the ventral surface of the egg. As to the other parts of the embryo, differences are distinctly pronounced. In the *Bdellostoma* embryos (figs 51 and 53) the tail end of the embryo does not reach the posterior pole of the egg, whereas in the *Myxine* embryo it reaches the posterior pole. The embryonic plate of the *Myxine* embryo is much broader than that of *Bdellostoma,* covering almost the entire part of the egg that is visible from the dorsal aspect. These differences are probably correlated to the fact that the eggs of *Myxine* are considerably shorter than those of *Bdellostoma.*

Fig. 5. The younger *Myxine* egg with embryo, ventral view. Eggshell removed.

My older embryo corresponds to a stage lying somewhere between DEAN's figures 53 and 58, but nearer to 53 than to 58. The tail end of my *Myxine* embryo, however, bends over the caudal pole of the egg, whereas that of these *Bdellostoma* embryos not reach as far as the pole.

My two embryos of *Myxine* belong to that group of embryos which DEAN indicates in *Bdellostoma* as late embryos: "Those in which the head region is well uplifted from the yolk-sac and in which, accordingly, the gill-slits have come to take their position on the sides of the neck. In this stage the barbels become conspicuous, the tail is a distinct narrow prolongation of the trunk and is overgrowing the yolk sac."

The *Bdellostoma* stage figured in DEAN's plate XXV fig. 124 (and plate XVIII, fig. 51) is characterized as follows: "Especially clear in this aspect ('lateral aspect') is the growth of the barbels and of the oral lobe-shaped outgrowth. The position in which the nasal opening will shortly appear is indicated at *n.o.* and from this point the Nasenrachengang may be traced in the preparation as far as its opening into the mouth cavity at *n. p.* The present stage contrasted with fig. 123 shows the continued backgrowth of the row of gill clefts and their divergence from the most anterior one of the series I. The foremost one of this row of gill clefts is now almost as widely removed from the first as the latter is separate from the eye. We note in this figure the greatly increased size of the myomeres, the line of whose lowest margins, however, is distinctly seen above the gill clefts. We note further that the thin-

Fig. 6. The older *Myxine* egg; shell removed, ventral view.

walled gill slits of the preceding stages are now becoming converted into the vascular pouches of the adult Cyclostome."

DEAN's stage fig. 126 differs from the preceding as the neck region is considerably longer and the region of the gills has been removed further caudad (in the figure beginning opposite the 19th myotome). The 1st gill-slit is no longer visible. The muscle plates have grown down considerably, reaching to the row of gill-slits. The first skeletal elements have appeared in the postorbital region.

My *Myxine* embryos correspond to stages lying somewhere between these two *Bdellostoma* stages, nearer to the second than to the first.

## 4. THE HEAD.

VOL
27
194

According to all figures of *Bdellostoma* embryos but one, the head region and the dorsal and lateral sides together form an evenly convex line. Moreover, the anterior pole of the head is rounded. The only exception from this general rule is the stage represented by fig. 125 in plate XXV of DEAN's work. At this stage, which is older than the two mentioned earlier (figs 124 and 126), the anterior part of the head seems to be covered by a cephalic shield, separated by sharp edges from the mouth portion of the embryo. This "shield" contains the eye and continues caudad into the gill region, where the gill openings seem to be situated on its lateral part. As the somewhat older embryos in figs 127 and 128 have no trace of such a shield and as fig. 125 shows a very marked shrinkage, it is not impossible that the "shield" is an artefact produced by the shrinkage or even the drying up of the embryo. Possibly it is the large nasal sac that has collapsed, causing the deep cleft between the dorsal surface and the mouth portion. This cleft, then continues perhaps on both sides of the head and trunk as a very deep artificial groove. Compare fig. 8 of my older embryo, which shows a similar skrinkage. This at any rate is the interpretation I am obliged to give to this stage of DEAN, though it does not follow that this artefact cannot be based upon a morphological condition. See further below. pg. 11.

As in *Bdellostoma,* the head and neck region of the *Myxine* embryos is sunk down in a deep groove of the yolk (fig. 7, 8, 9) of the embryo, so that the upper surface of the embryo lies at the same level as the outline of the yolk surface. The surface of the head is rounded in the same way as the surface of the yolk. In *Myxine* this upper convex surface of the head is bordered frontally and laterally by a thin laterally projecting sharp fold (fig. 7, 9, 12 *b.c.s.*), which forms an edge around the anterior and lateral borders of the head. Caudally this fold extends a considerable distance along the dorsal portion of the neck and trunk, dorsally to the gill region. The fold issues

about on a level with the middle portion of the myotomes — not at their lateral (lower) border. Caudally the fold could be followed over the anterior pole of the egg to the point where the rudiment of the trunk broadens to cover the main part of the dorsal surface of the yolk. This point corresponds to the point at which the ventral surface of the head region bends over in the ventral yolk-mass. The caudal limit of the free part of the embryo is an obliquely placed line or plane, lying caudally to the gill region. It can be said therefore that the fold ends just behind the gill region of the trunk. Thus there is a "head-shield" present covering the head and trunk to a point past the branchial region. This head-shield does not correspond to that depicted by DEAN, which, according to his figure 125, contains the eye and the branchial openings. A similar "shield" to that in DEAN's figure, is present in my older *Myxine*-embryo, but there it is decidedly a product of shrinkage which has caused the formation of a deep cleft at the lower margin of the myotomes. My specimen is not so strongly shrunk as that of DEAN. Consequently the the eye and the branchial apparatus have not been drawn into this cleft, as they apparently have in DEAN's specimen.

Fig. 7. The younger *Myxine* embryo, lateral view.

Fig. 8. The older *Myxine* embryo, lateral view.

Fig. 9. The head of the younger *Myxine* embryo, seen from in front.

As already stated, DEAN's figures of the *Bdellostoma* embryos do not show any lateral fold (excepting in fig. 125, already discussed). Nevertheless such folds are present already at a stage where five gill-slits are present, the first of which lies in front of the auditory capsule. It is possible to make this statement after examining the photographs published by CONEL (1931) in his paper on the development of the brain of *Bdellostoma stouti*. In his embryo 11, corresponding to DEAN's figs 31, 94 and 100, the fold is seen in the transversal sections depicted in figs 33, 34 and 35. The fold is also visible in

CONEL's figs 76—88. These figures are photographic reproductions of transverse sections of his embryo No. 77, corresponding to DEAN's figures 47 and 113, being from a stage with 12 gill-slits. Similar folds are also seen in his embryo No. 2266. This embryo corresponds with DEAN's stage figs 60, 108 and 126. In NEUMAYER's (1938) "Stadium I" of *Bdellostoma,* corresponding (according to NEUMAYER) to DEAN's stage fig. 122 (I believe, however, that it is considerably older, perhaps corresponding to DEAN's fig. 124), the fold is not so sharply defined as that of *Myxine,* and therefore it might have been overlooked in the total mounts used by DEAN.

STENSIÖ (1927) has devoted a chapter to a phylogenetical discussion of the *Myxinoidea.* In this chapter he says: "And, finally, it is highly interesting to find that in certain stages the general appearance of the embryo in a lateral view was very suggestive of a Pteraspid." The embryo to which he refers is even the embryo of *Bdellostoma* depicted by DEAN in his fig. 125. My interpretation of this embryo makes it less suggestive of a Pteraspid. Nevertheless the myxinoid embryo undoubtedly has some resemblance to a Pteraspid, when the conditions of the head-shield which I have described are considered. This shield lies dorsally to the eye and dorsally to the gill-slits and ends caudally behind the branchial region (fig. 13 *b.c.s.*) Thus in my *Myxine* embryos it has the same position and extension as the cephalic shield of a Pteraspid. Unfortunately the caudal extension of the shield is not known in earlier stages of development.

A comparison between a Myxinoid and a Pteraspid at once reveals a great difference in the position of the branchial region, which is far removed from the skull in the Myxinoid but not in the Pteraspid. In the very young embryo of *Bdellostoma,* however, the row of gill-slits begins already in front of the auditory vesicle. Then the foremost gill-slit closes and the rest of the row is successively removed further and further from the head. It may then be asked: Is it the branchial region that moves caudad or is it the prebranchial region that is prolonged? It is *a priori* obvious that the latter is the case as the branchial pouches are fixed partly to the intestine and partly to the skin. In a young embryo with five gill-slits the row of differentiated myotomes ends a good distance behind the auditory vesicle and is continued frontad by a frontally successively attenuated string of mesoderm in the posterior part of which new myotomes are differentiating. New myotomes successively develop and thus the neck grows longer, because the free part of the anterior portion of the body is more or less fixed caudally to the yolk-sac, which does not shorten to any appreciable extent. At a stage with seven gill-slits the foremost myotome lies only just behind the auditory capsule. At the anterior end of the row of mesoderme segments there is thus a growth zone from which new segments develop. In my *Myxine* embryo, in which there are 11 or 12 well developed myotomes in front of the branchial region, the foremost segment



VOL
27
194

is undifferentiated frontally, there apparently producing new segments, which cause the prolongation of the neck. In a 140-mm specimen the first gill-sac lies inside the 18th segment. (Corresponding to about to the 15th in the embryo.)

This lengthening of the neck must be considered a secondary character. Thus, in the ancestors of the Myxinoids the gill region followed immediately behind (or partly below) the skull, as in the young *Bdellostoma* embryo, and together with the skull was covered by a head-shield, as in the Pteraspids. So long as this shield consisted of a dermal skeleton plate, no considerable prolongation of the neck region could occur. Supposing that the ancestors of the Myxinoids were Pteraspids or any kindred group of archaic fishes, the Myxinoid development must have been preceded by a reduction of the dermal skeleton; otherwise the prolongation of the prebranchial region could scarcely have taken place.

Concealed below the anterior part of the "head-shield" lies the "face" of the embryo (fig. 7, 8). It is sunk into a deep cleft in the yolk-mass of the ventral part of the embryo. On a side view it forms a broad triangle, at the tip of which the three semihemispherical rudiments of the tentacles are seen. Behind the posterior tentacle a transverse groove indicates the position of the future mouth opening, delimited caudally by a distinct swelling. Viewed from the front (fig. 9), the "face" forms a quadrangular surface dorsally only a little narrower than the shield, while ventrally it is narrower than dorsally, square-cut, with a rather broad medial lobe on each side flanked by the two anterior tentacles. From below is observed the group of tentacles, of which the nasal tentacles lie medially distinctly behind the point where the future nasal opening will later appear. The first and second lateral tentacles lie laterally to the nasal, the first on a level anterior to the latter. Medially to the second lateral tentacle a slight swelling is seen extending nearly to the midline. This swelling probably represents a third lateral tentacle. All tentacles lie in front of the level of the oral membrane i.e. preorally. The location of the tentacles is about the same as in *Bdellostoma*, the differences being such that they may be interpreted as being due to shrinkage. The mouth opening is still closed, but the place where it will later break through is marked by an oral membrane. This is transverse, lying behind the tentacles, as stated by DEAN to be also the case in *Bdellostoma* embryos.

## 5. THE SKULL OF THE ADULT *MYXINE*.

Before we enter upon a description of the embryonic skull of *Myxine* it seems suitable to give a short account of the adult skull (fig. 10).

The neuro-cranium consists of the so-called parachordals with the auditory capsules and the trabecles. The latter extends as separate rods frontad to join

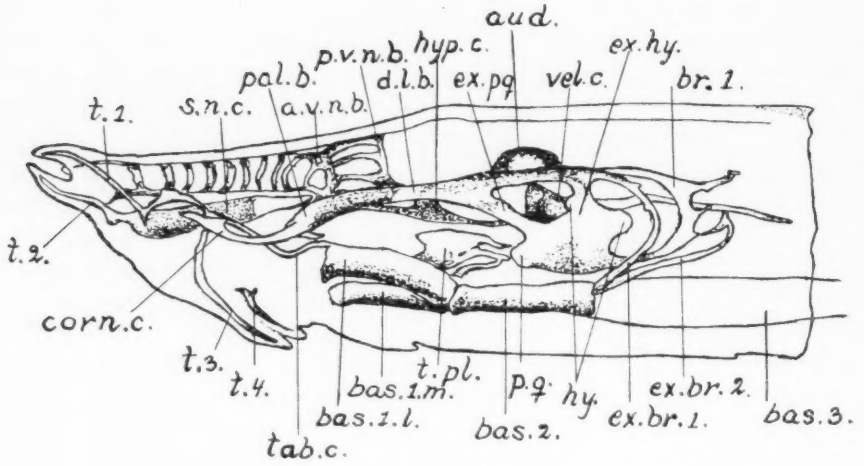


Fig. 10. Skull of adult *Myxine*.

the "palatine bar" of COLE (1905). The hypophysial plate is connected with the trabecles by a short bridge on each side. These bridges are connected with the postero-ventral corners of the nasal capsule by means of cartilage bars. Along the basis cranii, and at a short distance from it, runs laterally a longitudinal cartilage bridge, of which the frontal part bends mediad, forming a commissure: the "palatine bar". The subnasal cartilage with the cartilages of the second tentacle is connected with the dorsal surface of this commissure. At the fronto-lateral end of the palatine bar issues the "cornual" cartilage. On the lower side of the palatine bar sits the strong horny palatine tooth. The longitudinal bridge is connected with the neurocranium by three short cartilaginous connections, one at the posterior part of the auditory capsule, one in front of this capsule and one with the trabecula at about the point where the hypophysial plate has its connection. With the longitudinal bridge is connected the visceral arch system. Two "branchial arches" connect up with the postotic part of the bridge. These are the arches I and II. In front of these lies a large cartilaginous lateral plate, which is connected with the longitudinal bridge by broad cartilage bands of which the posterior is fastened on a level with the posterior part of the auditory capsule, the anterior on a level with its anterior part. The second branchial arch is connected with the posterior lower corner of the lateral plate, whereas the first arch is connected with the middle piece of the basal skeleton, to which an incomplete third branchial arch is also connected. The posterior half of the lateral plate is called by COLE (1905) the "Hyoid" arch and the anterior part the "Pterygoquadrate". On the posterior border of the "hyoid" arch is a broad process, and on its anterior border another similar but smaller process is present (absent in *Bdellostoma*?).

On the anterior, lower border of the "pterygoquadrate" a broad frontally directed process is developed. The basal skeleton consists of the three well-known sections: the posterior, the middle and the anterior. The anterior segment consists, on each side, of the external and the internal basal bar, of which the external carries the "labial" cartilage with the cartilages of the first and third tentacles. The middle section is paired, the posterior unpaired. It may be pointed out that there are many variations in the behavior of the "branchial" arches, consisting of differently developed processes thereon.

## 6. THE SKULL OF THE EMBRYO.

The development of the myxionid skull is known only from the posthumous work of NEUMAYER, edited in 1938 by H. MARCUS. NEUMAYER obtained two embryos and a newly hatched young specimen of *Bdellostoma stouti* from the collection of DEAN. His stage I is said to correspond to DEAN's figures 48—50, 104 and 122 respectively. His stage II corresponds to DEAN's figures 57, 58, 59 and 106. As to development, my *Myxine* stage is older than stage I and younger than stage II. The newly hatched stage is NEUMAYER's stage III.

In stage I, cartilage and procartilage are already present at different places. In his reconstructions NEUMAYER has only reproduced such skeletal elements as are clearly cartilaginous, even if the cartilage is young. But he has omitted such mesenchymatic rudiments as are not clearly procartilaginous or cartilaginous. The model of his first stage therefore looks very incomplete, certain parts lacking which must undoubtedly have been present as a more or less advanced rudiment.

In *Myxine*, as in *Bdellostoma*, the auditory region of the skull may be termed a centre of chondrification (NEUMAYER). In my specimen of *Myxine* the only really chondrified parts of the skull are the auditory capsules; all other skeletal elements are prochondrial or mesenchymatic, the prochondrial more or less connecting up with these capsules.

### A. THE BASIS CRANII AND THE AUDITORY CAPSULES.

In this part I propose to consider the notochord, the parachordals, the auditory capsules and the trabecles (with their dependants).

*The notochord.*

The notochord is remarkable for its long anterior portion, where the typical chorda-tissue is degenerating, the notochordal sheet in particular being preserved (figs 11, 12). The non-degenerated part of the notochord does not

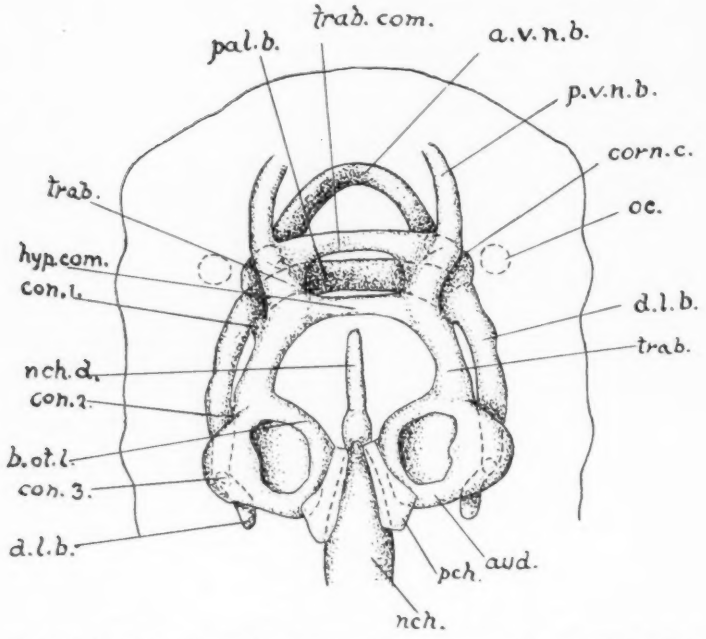


Fig. 11. Skull of *Myxine* embryo, dorsal aspect. Reconstruction from serial sections. 31 ×.

extend further frontad than to about the medial part of the auditory capsules, where it ends obtusely pointed. In front of this point, however, the notochord continues frontad as a very conspicuous string, nearly reaching the hypophyse. The notochordal hook, according to KUPFFER present in younger embryos of *Bdellostoma*, is also present in my *Myxine* specimen (fig. 12). Such a degenerating part of the notochord is likewise present in *Bdellostoma*. It was demonstrated by KUPFFER (1906) in his figure 30. NEUMAYER (1938) has apparently omitted it in his reconstructions of his stages.[1]

In my 43 mm specimen such a degenerating notochordal tip is also present, but it is much shorter than in the embryo. A 100 mm specimen, moreover, has a similar but even shorter degenerating anterior notochordal tip. It lies immediately dorsally to the arteria vertebralis capitis.

*The parachordals and the basiotic lamina.*

The parachordals of NEUMAYER's stage I of *Bdellostoma* are said to consist of the thickened medial rim of the auditory capsule. This rim is caudally (parachordale posterius) connected with its *vis-à-vis* by a prochondrial bridge dorsally to the notochord. Frontally it passes beyond the auditory capsule,

[1] In the reconstructions of stage II the anterior tip of the non-degenerated part of the notochord, demonstrated in his sections figs 13 and 14, has also been omitted.

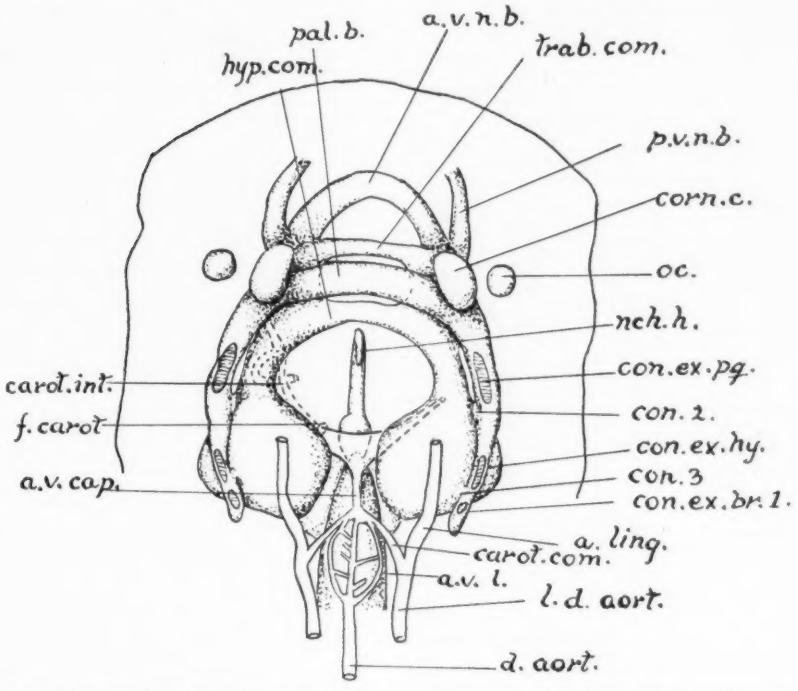


Fig. 12. Skull of *Myxine* embryo, ventral aspect. Reconstruction from serial sections. 31 ×.

forming a short parachordale anterius. NEUMAYER compares these conditions with those in *Lepidosteus, Amia* and *Teleostians*. VAN WIJHE (0000) had already suggested that what STÖHR (1892) named the anterior parachordals, in *Amia* are not parachordals at all but the lamina basiotica with which the polar cartilage and the trabecles are connected. According to this interpretation the parachordals are represented by the posterior parachordals only. I have studied (1943) the parachordal question in *Salmo salar* (with the conditions similar to those in *Amia* and *Lepidosteus*) and found that VAN WIJHE's interpretation is correct. In Selachians I have found that the polar cartilages and trabecles never join the parachordals direct (HOLMGREN, 1940), the lamina basiotica there playing a more important rôle in the formation of the anterior part of the basis cranii, especially in the *Batoidei*, than the parachordals.

If one considers the conditions in *Myxine* from these points of view, the interpretation of the parachordals must theoretically differ from that of NEUMAYER, viz. the "posterior parachordals" represent the entire parachordal system (figs 11, 12, 19, 23, 24, 25 *p.ch.*), the rim of the auditory capsule the lamina basiotica and the anterior parachordals, possible the polar cartilages (or posterior part of the trabecles). Fortunately my *Myxine* embryo substantiates this interpretation. In this embryo there is a distinct cell mass (figs

24, 25 *p.ch*) between the notochord and the auditory capsule. This mass forms the rather strong parachordal portion behind the auditory capsule, and from this part it could be followed uninterrupted to a level with the tip of the non-degenerated notochordal portion. Outside this parachordal tissue lies the thickened rim (figs 11, 25 *b.ot.l.*) of the auditory capsule. The rim thickens in the portion behind the notochordal tip, through the addition of cells from the lateral border of the parachordal. In front of the notochord no such addition occurs. In NEUMAYER's stages the parachordals have already joined the rim of the auditory capsule so completely and intimately that it probably could not be differentiated from it. (*Bdellostoma* seems to develop its parachordals earlier than *Myxine;* thus in NEUMAYER's stage I the parachordals are already joined dorsally to the notochord and, in addition, have rudiments of basidorsals and basiventrals.) Supposing that the skull is built up on the same general scheme as that of the other lower vertebrates, it must have had a lamina basiotica and in that case the border portion of the auditory capsule must represent this lamina. The auditory capsule in my specimen does not deviate markedly from that in *Bdellostoma* as described by NEUMAYER, but it is developed more in the horizontal plane than in *Bdellostoma,* and the auditory opening faces almost directly dorsad.

VOL.
27
194

*The trabeculae.*[1]

The trabecles, as already stated, issue from the anterior end of the basiotic "lamina". As the basiotic laminae diverge strongly frontad, the posterior ends of the trabecles are separated by a wide space. The trabecles converge (figs 11, 12 *trab.*) rather strongly frontad to a point somewhat behind the level of the eye. From there a strong commissure issues joining the two trabecles to one another (figs 11, 12, 17 *hyp.com.*). The trabecles, however, continue in front of this commissure. Now they are about parallel with one another for a short distance, finally bending mediad and joining in a second, rather diffuse commissure (figs 11, 12, 14 *trab.com.*). The naso-hypophysial tube (fig. 17 *d.n.h.*) lies dorsally to the two commissures. On a comparison with NEUMAYER's stage II it is very clear that the posterior commissure represents the rudiment of the hypophysial cartilage. Then the anterior commissure must be the trabecular commissure as present in other vertebrates. The posterior trabecular comisssure seems strange and unfamiliar to the general vertebrate scheme. Nevertheless, there are, at least in Selachians, in addition to the "normal" trabecular commissure one or two other commissures present, viz. the precarotid and the postpituitary commissures, which join a medial cartilage nucleus already described by VAN WIJHE. This cartilage divides the polar fenestra in a posterior part: the anterior basicranial fenestra, and an anterior:

[1] In HOLMGREN and STENSIÖ (1936) p. 287, fig. 232 the connotation *v. trab.* and *h. trab.* is erroneous as the trabeculae are not seen at all in this figure.

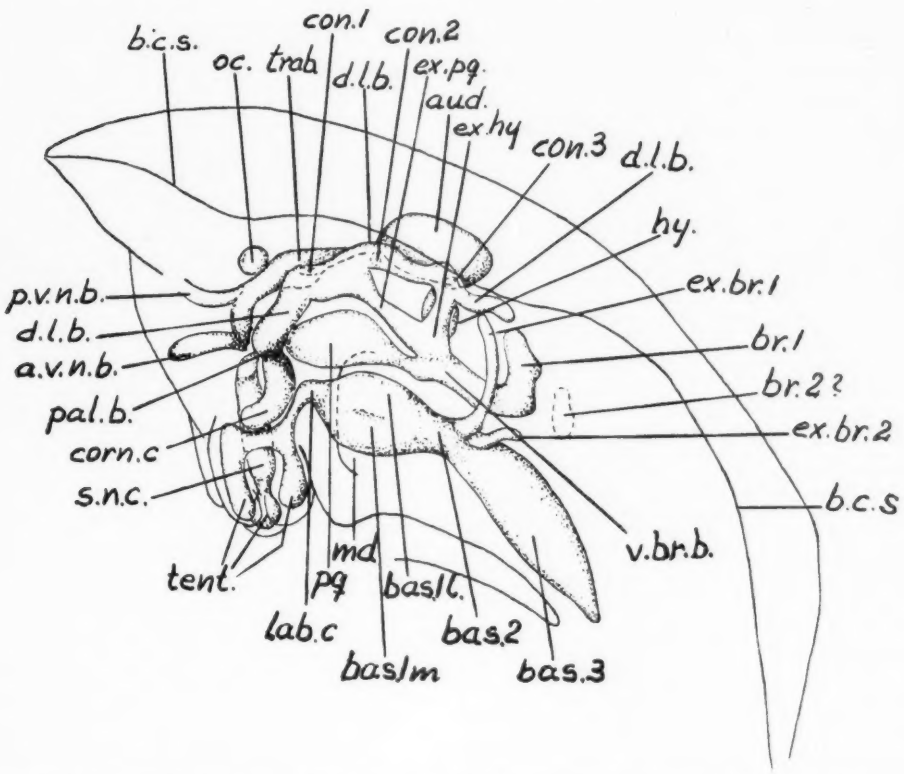


Fig. 13. Skull of *Myxine* embryo, lateral aspect. Reconstruction from serial sections. 31 ×.

the hypophysial fenestra. This cartilage together with the bridges which connect it with the trabeculae, corresponds in my opinion to the hypophysial commissure in *Myxine* or the "hintere Gaumenplatte nebst Verbindungsknorpel" of NEUMAYER. If the preceding homologization — the only possible one — is acceptable, a certain light may be thrown upon the question of the polar cartilage in *Myxine*. In the Selachians the posterior commissures are always connected with the polar cartilage, the development of which has been followed in sharks and rays (HOLMGREN, 1940). There the polar cartilage is short, so that the commissures lie in the posterior part of the polar fenestra. Is the commissure in *Myxine*, homologous with those in Selachians, it seems to follow that the part of the trabecular system to which they belong is also homologous, i.e. that the posterior part of the trabecles with the commissure in *Myxine* belongs to the polar cartilage. Then the trabecle *sensu strictiori* must be the anterior part of the trabecular system in front of the hypophysial commissure. This question, however, cannot be definitively answered before the early development of the trabecles has been investigated in *Bdellostoma* or *Myxine*.

As will have been seen from the preceding pages, I have not adopted NEUMAYER's terminology of the trabecular system. He follows SEWERTZOFF's interpretation of the trabecule of *Petromyzon* as representing "parachordal horns". SEWERTZOFF's interpretation was based upon KOLTZOFF's investigation of the early development of the skull in *Petromyzon*. He found that the trabecles of *Petromyzon* were somitic (ento-mesodermic) in origin, and according to SEWERTZOFF could not therefore represent any trabecles which were thought to be of ecto-mesodermic origin. KOLTZOFF's statement as to the origin of the trabecles has recently been rejected by DAMAS (1943), who states that the trabecles of *Petromyzon* are really derived from the ecto-mesoderm. On the other hand, my researches into Selachians indicate the probability that their trabecles contain at least a core of somitic origin, and my investigations into the origin of the trabecles in *Salmo* and Ganoids have shown that these trabecles really have a somitic origin. (MATVEIEFF's results also indicated that the main part of the trabecles in Selachians and in *Acipenser* are somitic.) In (Dipnoi? and) Amphibians at least a posterior part of the "trabeculae" is somitic. From this short survey it seems conclusive that at least a part of the trabeculae is generally of somitic origin. According to DAMAS, *Petromyzon* would then be the single exception from this rule. His investigation is very carefully conducted, but so is that of KOLTZOFF. Nevertheless they have arrived at quite opposite results. I too have tackled the trabecular problem of *Petromyzon*, but gave it up. At one time I thought I could accept KOLTZOFF's views, but again I felt more inclined to contest them. I think that the trabecular problem of *Petromyzon* is not yet solved. Whatever the ultimate result regarding *Petromyzon* may be, the interpretation of its trabecles as parachordal horns cannot be correct whether the "trabecles" are ecto-mesodermic or whether they are somitic in origin. If they are mesenchymatic they cannot belong to the parachordals, which are somitic, and if they are somitic they behave like the normal trabeculae of lower vertebrates.

It is seen from a lateral view that the trabecles (fig. 13 *trab.*) bend in a ventral direction, so that the trabecular commissure lies much more ventrally than the hypophysial. This position is correlated to the ventral position of the future nasal and oral openings.

## B. THE NASAL CAPSULE AND DUCT.

The nasal capsule of my *Myxine* embryo is entirely mesenchymatic. Nevertheless its general shape can be determined. In front of the hypophysial commissure the trabecle seems to be continued frontad in the form of a mesenchymatic rod, not very well outlined and frontally without any boundary merging into the mesenchyme surrounding the nasal sac. This rod is the



VOL
27
194

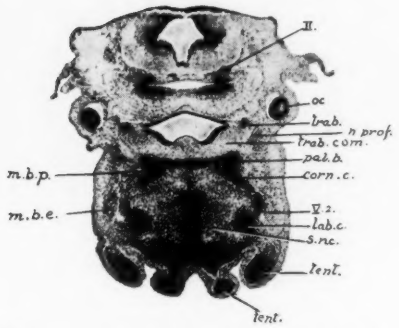


Fig. 14. Transversal section of the head, taken through the eyes and the trabecular commissure (section 105 of the series). 20 ×.

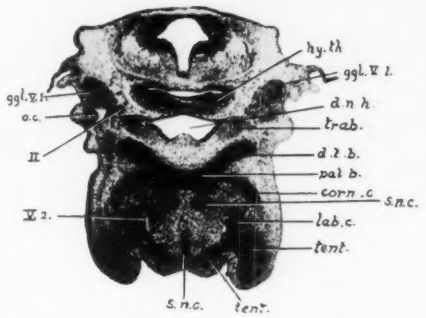


Fig. 15. Transversal section of the head, taken just behind the eyes (section 112 of the series). 20 ×.

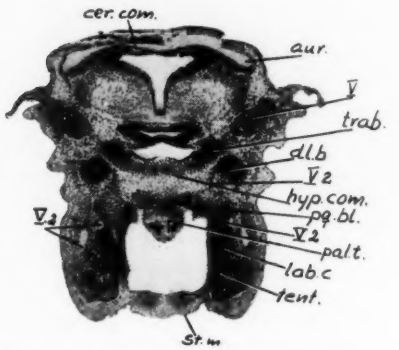


Fig. 16. Transversal section of the head, taken through the hypophysial commissure and the palatine tooth (section 124). 20 ×.

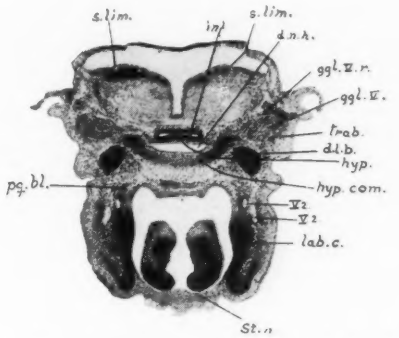


Fig. 17. Transversal section of the head, taken through the frontal part of the dental plate and the hypophysial commissure (section 130). 20 ×.

rudiment of the posterior border cartilage (arcus posterior, NEUMAYER) of the future nasal capsule (figs 11, 12 *p.v.n.b.*). From the ventro-lateral portion of the mesenchymatic trabecular commissure here issues at about right angles to the commissure a similar but better defined rod which is connected with its *vis-à-vis* in front of the nasal sac. This rod is the rudiment of the anterior border cartilage (figs 11, 12 *a.v.n.b.*) (arcus anterior, NEUMAYER) of the future capsule. These two rods thus mark the upper (posterior) and lower (anterior) borders of the nasal sac. This sac has a number of deep external folds answering to internal ridges. These external infoldings are filled up with a dense mesenchyme, which contains the material for the longitudinal cartilaginous bars characterizing the future capsule. These rudiments are continuous with the rudiments of the posterior and anterior border-cartilages. The nasal tube is surrounded by a thick mesenchymatic tube: the rudiment of the nasal cartilages and connective tissue surrounding it.

The subnasal cartilage (figs 13, 14, 15 *s.n.c.*) may also possibly be regarded as belonging to the nasal skeleton, though there is no relation between it and the nasal skeleton other than their proximity to one another. In the *Myxine* embryo the subnasal "cartilage" is quite mesenchymatic, though rather distinctly outlined. Its anterior (lower) part is divided into two branches, one to each of the so-called tentaculae II. The posterior (upper) end of the cartilage also has two lateral branches, which are in some way connected with the palatine commissure or bar (AYERS and JACKSON, COLE [ethmoid (PARKER), "vordere Gaumenplatte" (NEUMAYER)], (see below).

## C. THE VISCERAL SKELETON.

The visceral skeleton of the embryo consists of the so-called pharyngeal basket (with branchial arches of some sort), the velar skeleton, the dental plate skeleton and the basal skeleton.

The pharyngeal basket consists of a longitudinal dorsal rod (figs 11, 12, 13, 16—25 *d.l.b.*) or bar, running parallel to the trabecular system and the lower side of the auditory capsule, passing beyond it caudally. This longitudinal bridge may be divided into a posterior, an auditory and a trabecular part. Frontally, behind the trabecular commissure, the longitudinal bridge meets its *vis-à-vis* in a strong commissure, the "palatine bar" (figs 11—15 *pal.b.*). The bridge has, as in the adult, connections with the neurocranium at three points (con 1, 2, 3), viz. with the ventrolateral part of the auditory capsule, with the trabecle immediately in front of the auditory capsule and with the trabecle on a level with the hypophysial commissure. The nature of these connecting bridges could not be clearly defined. The auditory connection seems to be established, at least structurally, by a local thickening of the wall of the auditory capsule joining the longitudinal bridge. The posterior trabecular connection seems to be formed by a rudiment, which is structurally differentiated from the trabecle as well as from the longitudinal bridge, and which may possibly correspond to the so-called pedicle process of the trabecle of the *Ammocoetes* larva of *Petromyzon*, a process which according to SEWERTZOFF (1916) has a separate origin.[1] The anterior trabecular connection is decidedly of trabecular origin, perhaps a sort of a trabecular horn. These statements do not agree well with an interpretation of these connecting bridges as being dorsal parts of visceral arches.

From the lower median part of the commissure ("palatine bar") of the longitudinal bridges issues the rudiment of the cornual cartilage (figs 11—15 *corn.c.*). It is possible that the two cornual cartilages are connected by a commissure of their own below the bridge commissure, but that cannot be regarded as certain.

[1] Compare however pg. 30.

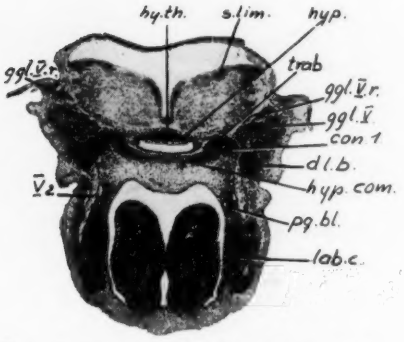


Fig. 18. Transversal section of the head, taken through the posterior part of the hypophysial commissure and the hypophysis (section 138). 20 ×.

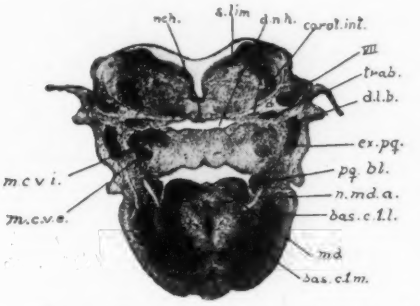


Fig. 19. Transversal section of the head, taken through the degenerating tip of the notochord and the extrapalato-quadrate (section 164). 20 ×.

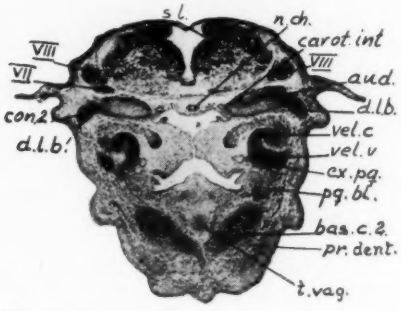


Fig. 20. Transversal section of the head, taken through the anterior border of the auditory capsule (section 185). 20 ×.

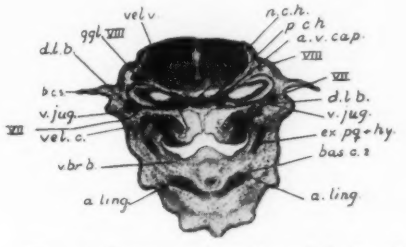


Fig. 21. Transversal section of the head, taken through the tip of the not degenerating tip of the notochord (section 195). 15 ×.

With the longitudinal bar are connected: the "first branchial arch" (figs 13, 23—25 *ex.br.1.*) the "hyoid" (*ex.hy.*) and the "pterygo-quadrate" (*ex.pq.*). Thus the second (*br.1.*) and third (*ex.br.2.*) branchial arches have no connection with the bar. Nor has the third arch of the adult any such connection, and it is therefore of less interest in the embryo, but the second has such a connection in the adult. In my embryo it is clearly seen that the second arch is formed immediately outside the lining epithelium (figs 26, 27 *br.1.*) of the entodermal gut and is thus a true branchial arch fully comparable with those of the gnathostome fishes. The first and third arches, on the other hand, are developed in a more superficial position well removed from the gut. They are thus external arches. The fact that the third arch does not reach the dorsal longitudinal bar indicates that this arch is dependent upon the basal skeleton. Moreover, the conditions of the first branchial arch justify the conclusion that the same is also the case in regard to this arch. Its junction with the

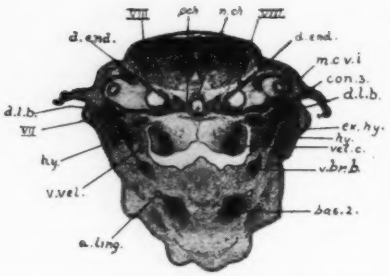


Fig. 22. Transversal section of the head, taken through the level of the ductus endolymphaticus, and the hyoid (section 212). 20 ×.

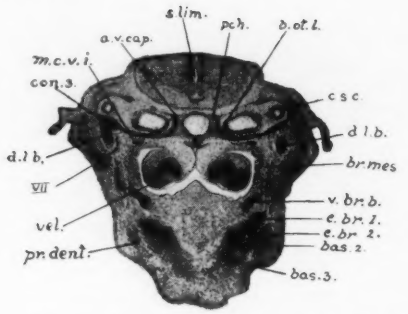


Fig. 23. Transversal section of the head, taken through the connection 3 of the dorsal longitudinal with the auditory capsule (section 222). 20 ×.

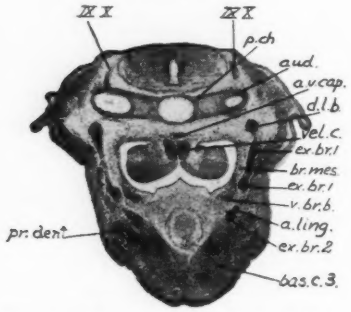


Fig. 24. Transversal section of the head, taken through the most posterior part of the auditory capsule (section 234). 20 ×.

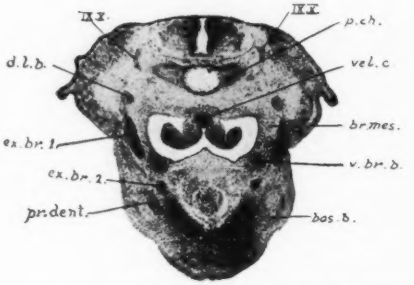


Fig. 25. Transversal section of the head, taken through the parachordals, just behind the auditory capsule (section 240). 20 ×.

longitudinal bar is not complete as there are structural differences which indicate that this junction is a secondary one. The conclusion to be drawn from this evidence is that the first and third branchial arches belong to a different series of visceral "arches" than the second: they are extra-branchial arches comparable with the inferior extra-branchials in Gnathostomians. If we accept this view, it is necessary to revise our conception of the extra-branchials in Selachians. These I have previously considered to be special branchial rays, an interpretation which I am now inclined to with-draw, as they belong to a layer external to that of the true branchial arches.

As I have already stated, the second arch develops just at the epithelial lining of the branchial gut. It there develops in a mesenchymatic layer which covers the sides of the gut (figs 23—25 *br.mes.*). This layer, which is present along the entire branchial part of the gut, thickens rather abruptly where the narrow posterior part of the branchial intestine widens on a level with the posterior end of the velar fold. From that point frontad the mesenchymatic layer retains a certain thickness, and it is in this layer that the second arch



VOL
27
194

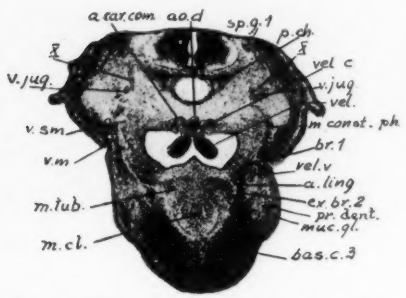


Fig. 26. Transversal section of the head, taken somewhat behind the fig. 25 (section 245). 20 ×.

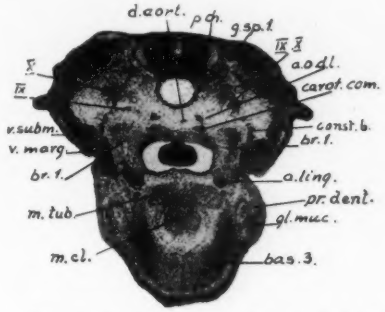


Fig. 27. Transversal section of the head, taken through the first branchial arch (section 252). 20 ×.

develops. Behind this arch the layer is thinner, subsequently thickening again about on a level with the end of the velar fold. There the thickening seems to indicate the presence of another arch rudiment (fig. 13 *br.2?*). The possibility of such an arch is sustained by the fact that in a newly hatched specimen of *Bdellostoma* NEUMAYER has found a well-developed fourth arch, about on a level with the posterior end of the velar skeleton. The mesenchyme layer in which the internal branchial bars develop I propose to call the branchial mesenchyme.

In front of the anterior internal branchial bar the branchial mesenchyme continues frontad. At the lower border of this mesenchyme a distinct thickening or bar (figs 13, 22—25 *v.br.b.*), caudally continuous with the first arch, extends frontad to join the lower caudal corner of the so-called "hyoid" arch of COLE. Where the bar joins the "hyoid" it forms the ventral part of the mesenchyme, located internally to the "hyoid", which does not belong to this mesenchyme but to a tissue portion lying outside it. The branchial mesenchyme inside the "hyoid" is generally not very thick, but inside the upper part of the "hyoid" the mesenchyme is strongly thickened, densely nucleated, forming a large pad frontally and caudally overlapping the "hyoid". This pad (figs 13, 22 *hy.*) is about to join the prochondrium of the "hyoid". In this pad, which belongs to the branchial mesenchyme, I see a rudimentary inner branchial bar: a real "hyoid" arch. In the preliminary reconstruction of these conditions, published in the third part of my work on the head in fishes (HOLMGREN, 1942) the internal "hyoid" bar was described and depicted as a complete arch obliquely crossing over the "hyoid". New investigations and reconstructions have, however, failed to demonstrate the distinct and direct connection of the pad with the horizontal bar behind the "hyoid" corner, seen in my preliminary reconstruction (p. 238). Actually the pad is connected with the horizontal bar only by means of the general branchial mesenchyme.

The longitudinal bar, after connecting up (fig. 12 *con.ex.hy.*) with the "hyoid"

(fig. 13 *ex.hy.*) (first prebranchial arch according to NEUMAYER), continues frontad into the "pterygo-quadrate" (*ex.pq.*) (second prebranchial arch according to NEUMAYER), which joins the longitudinal bar somewhat behind the connection of the latter with the trabecle (fig. 12 *con.ex.pq.*). The "pterygo-quadrate" and the "hyoid" belong to the external set of arches. They are therefore extra-branchial structures and probably correspond to dorsal extra-branchials, since they have no connection with the basal skeleton as have the first and third "branchial" arches (see above).

On the ventral border of the ventral branchial bar (already below the "hyoid") the cells are more loosely arranged than elsewhere on the bar. Frontad these cells form a distinct band of cells at the lining of the mouth cavity (fig. 13). Gradually this band grows higher and thicker and fills up the space between the dorsal longitudinal bar and the floor of the mouth cavity (figs 13 *pq.*, 16—20 *pq.bl.*). Frontally this tissue mass seems to end in an indistinct commissure behind the commissure (fig. 13 *pal.b.*) of the dorsal longitudinal ("palatine commissure") bars. On this indistinct commissure the rudiment of the palatine horny tooth is developing. I cannot find any other explanation of the described tissue mass than that it represents a palato-quadrate, which, however, never attain to any further development but reduces and disappears with the exception of small remnants at its caudal and frontal ends respectively. In our short description of the adult skull of *Myxine* was mentioned a broad process at the lower frontal border of the "pterygo-quadrate". This process (absent in *Bdellostoma*) probably represents the posterior part of the true palato-quadrate. In that part of the palato-quadrate which presumably forms a commissure a pad of mesenchyme forms a support for the horny tooth. This pad is probably (at least in part) a part of the palato-quadrate. Good support for this assumption is afforded by the observation of AYERS (1931, p. 340), according to which there are present in *Bdellostoma* two small symmetrically placed cartilages supporting the lens-shaped body in which the tooth is inserted. Meanwhile these two cartilages are united in the form of a crescent. AYERS considers that these two cartilages represent the palato-quadrate. In *Myxine* no such cartilages occur.

The rudimentary palato-quadrate is broadly connected caudally with the mesenchyme of the dental plate or lower jaw, in which, however, the cartilages are still so undifferentiated that a good reconstruction of them was not possible.

The velar skeleton of the two sides forms together a V-shaped cartilage of which the frontally directed limbs are clubshaped, hollowed out laterally and continous with the extra-palatoquadrate (figs 20—26 *vel.c.*).

The basal skeleton of the embryo already foreshadows that of the adult. The three parts of it are about to differentiate (fig. 13 *bas. 1, 2, 3*), but they are not yet delimited from one another. Nor are the paired parts of the anterior segments yet separated. The "labial" cartilages are short and end in



VOL
27
194

the bent-down bulky rudiments of the tentacular mesenchyme of the first and third tentacles. The mesenchyme of the fourth tentacle is connected with that of the third.

## 7. SOME POINTS OF RELATIONS BETWEEN THE CRANIAL NERVES AND THE VISCERAL SKELETON.

I have already (HOLMGREN, 1942) given an account of the relation between the cranial nerves and the visceral skeleton which are of primary importance for the interpretation of this skeleton. I will therefore merely recapitulate some of the more essential data.

The trigeminal, with the exception of the nervus profundus, after leaving the brain passes over the trabecula, entering between the latter and the dorsal longitudinal bar through the fenestra formed by the trabecula, the longitudinal bar and the two anterior bridges connecting up with the former. The trigeminal thus lies *internally* to the anterior part of the pharyngeal basket. The trigeminal branches run in a ventral direction and cross the rudimentary palato-quadrate mesenchyme on its *outside*, a fact that affords good evidence as to the correct interpretation of this rudiment. At the frontal edge of the "pterygo-quadrate" a broad process is present in the adult fish, as already mentioned. At its frontal edge, and covered by it on the outside, runs the mandibularis posterior nerve. It has not the typical position of a mandibular nerve which, if the process belonged to the internal visceral skeleton, as is maintained in the preceding pages, would run laterally to the edge of this process. But the condition in the embryo indicates that the process nevertheless belongs to an internal arch, viz. the mandibular arch. In the embryo the rudiment of the palato-quadrate is connected with the fronto-ventral border of the "pterygo-quadrate" and the mandibular nerve runs *outside* the connecting bridge. In the adult *Myxine* the broad process represents the connecting bridge of the embryo and thus contains the remainder of the palato-quadrate. If this is the case, the mandibularis nerve must have shifted from the outside of the process to its inside. The shifting of the nerve in relation to the process takes place late during the development, seeing that in a 43-mm specimen the nerve still runs outside the process, as in the embryo. In the adult the nerve runs inside the process just at its upper anterior corner, and then enters a thick ligamentous layer, which, being intimately connected with the process, covers its inside. This ligamentous layer continues ventrally to the process and then joins the basal skeleton. As the nerve has passed inside the process, it pierces the ligament lamella and comes to its outside, proceding in a caudal direction.

As there is no sensory-line system in *Myxine*, the lateralis system of the nervous system is almost absent. As no sensory facialis nerve is present the facialis

ganglion[1] either is absent or fused on to the trigeminal ganglion. (In *Bdellostoma*, which has a more or less developed sensory-line system, the trigeminus and the facialis ganglia according to NEUMAYER are intimately connected). The facial nerve of the *Myxine* embryo issuing from the brain in front of the auditory capsule enters the fenestra dorsally between the two commissures that connect the dorsal longitudinal bar with the auditory capsule region of the neural skull. From this fenestra the nerve turns caudad inside the "hyoid", passing dorsally to the mesenchymatic pad, i.e. the rudimentary hyoid arch on the inside of the "hyoid" of COLE. Behind this rudiment the nerve turns ventrad and crosses the bar mesenchyma behind the "hyoid" and the ventral longitudinal branchial bar on its *outside*, then turning caudad (and frontad) inside the first and third branchial arches but outside the level of the second. In the embryo the nerve soon comes in contact with the rudiment of the musculus cranio-hyoideus and then with the rudiment of the m. protractor cartilaginis basilaris posterior. In the adult the facial nerve gives off a strong branch to the m. cranio-hyoideus and a smaller one to the posterior as well as to the anterior protractor muscles. In the adult the nerve runs out caudally from the "hyoid" and then, after giving off the cranio-hyoideus branch, turns laterad and ventrad, crossing the posterior end of the "hyoid" on its outside. In the adult this crossing takes place far more anteriorly than in the embryo. This condition seems to be a consequence of the change of the position of the mouth, ventral in the embryo, terminal in the adult, which has caused the basal skeleton with its muscles (the protractors) ty shift to a frontal direction.

Thus the facial nerve (hyomandibular nerve) dorsally runs inside the "hyoid", then outside the branchial bar mesenchyma and the longitudinal branchial connecting-bar, innervating muscles belonging in part to the basal skeleton. The possible conclusion to be drawn from this evidence is that the "hyoid" is an extra-branchial of the hyoid arch and that the real hyoid arch lies inside it as the mesenchymatic pad, described in the preceding lines.

The glosso-pharyngeal and vagus nerves issue together from the brain. But soon after leaving the brain the two nerves separate and the glosso-pharyngeal pierces the rudiment of the musculus constrictor pharyngis and comes to its inside, where it passes somewhat posterior to the second branchial arch in the adult, innervating the constrictor muscle from its inside. The nerve thus lies outside the first internal branchial arch (second arch) and on the same level inside the first and third arches. Its position in relation to the first internal branchial arch indicates that it belongs to this arch, which thus corresponds to the first branchial arch of other fishes. Its position in relation to the first and third arches indicates that these are extra-branchials, as has already been concluded earlier from their other morphological relations.

[1] JANSEN (1930) found a small separate facial ganglion in *Myxine*.



VOL
27
194

## 8. INTERPRETATION OF THE MYXINOID SKULL.

NEUMAYER's interpretation of the skull of *Bdellostoma* is based on SEWERTZOFF's (1916) interpretation of the skull of *Petromyzon*. I shall therefore begin with a short summary of the latter.

SEWERTZOFF takes as his starting-point the conditions of the branchial basket in the *Ammocoetes* larva. It consists of vertically located branchial arches which are connected above and below the branchial openings by means of epitrematic and hypotrematic bars respectively. Dorsally each arch ends in a base (foot piece) leaning against the notochord, and ventrally the arches are connected on each side by a longitudinal cartilage bar. SEVERTZOFF's idea was that that part of the visceral skeleton which lies in front of the branchial basket was built up of metamorphosed branchial arches principally of the same construction as the arches of the branchial basket. On the basis of this idea he regarded the more or less vertically located pieces of the prebranchial region as visceral prebranchial arches, and the longitudinal pieces as epi- or hypotrematic cartilages. Thus the "extrahyal" is the first prebranchial or hyoid arch and its connection with the "epikeratohyal" and styliform process constitutes its epitrematic cartilage. The epikeratohyal + the styliform process was considered to be the second prebranchial (mandibular) arch to which the cornual cartilage belongs as its hypotrematic, the subocular arch as its epitrematic process. The anterior pillar of the subocular arch is, according to SEWERTZOFF, the third prebranchial (first premandibular) arch, and the bridge connecting it with the posterior side-plate is its epitrematic cartilage. The posterior and anterior side-plates were said to represent the fourth and fifth prebranchial (second and third premandibular) arches respectively.

However, some objections must be made to this attractive theory of SEWERTZOFF's.

1. The branchial arches of *Petromyzon* are external branchial arches, since their nerves and arteries run along their inside. In addition, the constrictor muscles lie on their inside. The first prebranchial arch, if developed homodynamously, must be an external arch and could not represent any hyoid arch, which is always an inner visceral arch with the hyoid artery and the hyomandibular nerve developed on its outside.

2. The bases (and the spine processes) of the branchial arches have been omitted from the theory in spite of their regular occurrence at the dorsal end of the external arches. The base, leaning against the notochord, has a frontal and a caudal limb between which the external arch proper is inserted. Comparing this with the "extrahyal" arch of the adult, we cannot help suggesting that SEWERTZOFF's "epitrematic cartilage" of this arch may perhaps be the anterior limb of its base, the posterior of which is represented by the dorso-caudally directed process on the caudal side of the arch.

3. The second prebranchial (or mandibular) arch offers great difficulties to the theory. It consists of three portions, of which the two lower are joined together by a short section of "soft" cartilage. The uppermost of these portions is apparently of a different origin from the two others as it belongs to the larval skeleton and is already present in the latter as the epikeratohyal or the pedicle process [barre vélaire primitive, DAMAS (1935)] of the posterior part of the trabecle. As far as I could ascertain from a great number of sections through embryos of 6—7 mm bodylength, the pedicle consists of cells proliferating from the trabecle in the space between the facial and trigeminal nerves. If this is the case, the pedicle may be a basi-trabecular process. The objection to such an interpretation, however, is that a basi-trabecular process, such as is present in shark embryos, is a process of the polar cartilage, which is somitic in origin, whereas, according to DAMAS (1943), the pedicle as well as the entire trabecle is ecto-mesodermal. KOLTZOFF (1902) found, however, the trabecle to be entirely somitic. I am not able to decide which of these two authors is correct. The second portion af the "mandibular arch" is the "styliform" process ("arc vélair", DAMAS, 1935). It is formed in the posterior part of the muco-cartilaginous ventrolateral plate of the larva along the insertion of the velum. The mandibularis branch of the trigeminal issuing from the trigeminal II ganglion in front of the pedicle turns inside the styliform process and runs ventrad towards the third portion of the arch. This portion is the "cornual" process (plaque infravélaire, DAMAS). I have once (1942) compared this cartilage with the dental plate in *Myxine*.

4. The subocular arch can scarcely be an epitrematic bar belonging to the second prebranchial arch as it is joined on to the pedicle process. Accepting the principle that the nerve of an internal arch must lie externally to it, the subocular arch — if part of an arch — must belong to an external arch.

5. Difficulties also arise concerning the anterior prebranchial arches. Whereas the trigeminal II runs inside the third and fourth "prebranchial arches", it runs outside the fifth, thereby demonstrating that the latter belongs to a set of "arches" different from the two others. In my opinion the fifth arch is a real internal arch, the two others belonging to an external system of cartilages.

NEUMAYER (1938) has applied SEWERTZOFF's ideas of the morphology of the *Petromyzon* skull to that of *Bdellostoma*. He has demonstrated that these ideas are quite applicable to *Bdellostoma* and he made a detailed comparison of the two skulls with special reference to the visceral skeleton. NEUMAYER's terminology is thus that of SEWERTZOFF. The dorsal longitudinal bar of the visceral skeleton is said to be composed of the epitrematic bars of the different arches. There are 3 or 4 branchial arches. The first and second prebranchial arches are connected by a broad hypotrematic bar, and so on.

The same objections as those raised against SEWERTZOFF's theory are valid

against its application to *Bdellostoma*. I shall therefore not enter upon a detailed explanation of NEUMAYER's attempt. I would merely point out that NEUMAYER apparently considered all the branchial arches to be of the same nature, which they are not, as I have explained in the preceding pages. There are present in Myxinoids external arches which are comparable with the "branchial arches" in *Petromyzon*, but which have no typical epi- and hypotrematic bars, and there are internal arches which have no corresponding parts in *Petromyzon*, in which all "arches" are external.

The remarks made in the preceding 5 paragraphs appear to serve as an adequate basis for new theories relating to a comparison between *Petromyzon* and Myxinoids.

The starting-points for my theory are:

1. All arches in *Petromyzon* are external.

2. There are in *Myxine* external as well as internal (true) arches.

3. The dorsal series of longitudinal bars in *Petromyzon* represent basal parts of external arches.

4. In the prebranchial part of the visceral skeleton no epi- or hypotrematic bars are present in *Petromyzon*, nor in *Myxine*.

5. The anterior pillar of the subocular bar of the adult *Petromyzon* is connected with the anterior part of the trabecle and is also connected with the trabecular commissure. The trabecle in newly metamorphosed specimens is seen as a core in the surrounding cartilage, which is continuous with the anterior pillar. Thus the anterior pillar of the subocular arch may be described as the inward-turning commissural anterior end of the subocular bar. The anterior pillar of the subocular bar may perhaps correspond to the short transversal cartilage bar, which connects the dorsal longitudinal bar with the trabecula in *Myxine* and the commissural part with the commissure of the longitudinal bars in the *Myxine* embryo.

6. The posterior lateral cartilage in *Petromyzon* is connected with the subocular bar at the point where this bar turns dorsad and mediad. In *Myxine* the dorsal longitudinal bar carries frontolaterally the so-called cornual cartilage in a corresponding way. The conclusion therefore seems possible that the posterior lateral plate and the cornual cartilage are homologous.

7. In *Petromyzon* the extrahyal arch is an external arch of the same nature as the external branchial arches. The hyomandibular VII nerve is related to it. In *Myxine* the so-called first prebranchial arch is an external bar related to the nervus facialis. It seems reasonable, then, to consider the arch in *Myxine* to be also an external arch, an extrahyal. In *Petromyzon* the second prebranchial arch is related to the mandibularis V nerve, which runs on its inside. The same is the case with the second prebranchial arch in *Myxine*. In both cases the named cartilage bars may represent external mandibular arches.

8. In *Petromyzon* the apicalis branch of the trigeminal II (sensory and

motor) runs inside the posterior but outside the anterior lateral plate. In *Myxine* the trigeminal II (sensory) runs inside the cornual cartilage but outside the so-called labial cartilage (which carries the cartilages of the first and third tentacles). From these statements we derive the following results: 1) a support for the interpretation already given in 6 that the posterior lateral plate in *Petromyzon* and the cornual cartilage in *Myxine* are homologous, and 2) the possible homology of the anterior lateral plate of *Petromyzon* with the labial cartilage in *Myxine*. The scarcity of evidence upon which these conclusions are drawn, however, makes them doubtful. 3) The possibility of interpreting the anterior lateral plate in *Petromyzon* and the labial cartilage in *Myxine* respectively as inner premandibular arches.

9. In the (old) *Ammocoetes* larva the big ventro-lateral plate of muco-cartilage is connected frontally by a strong bar with the muco-cartilage surrounding the trabecular commissure. This bar is called by DAMAS the "apophyse vestibulaire de la sangle ventrale". The two bars are located on each side of the mouth cavity, to which they give strong support. According to my interpretation this bar is the forerunner of the anterior lateral plate in the adult and should therefore correspond to the labial cartilage in *Myxine*. If this conclusion is correct, the so called basal plates of *Myxine* might in some way represent the ventro-lateral plate in the *Ammocoetes* larva. Carrying the comparison still further, we find that the ventro-lateral plate of *Petromyzon* has relations to the external visceral arches as it has in *Myxine* with the two extrabranchial arches. At present, however, this comparison cannot be carried further. But there is also another, probably a better, way of explaining the basal skeleton of *Myxine* on the basis of the conditions in *Petromyzon*. The basal skeleton in the *Myxine* embryo consists of three segments, of which the foremost is composed of two skeletal plates on each side, the middle of a paired and the caudal of one unpaired piece. In *Petromyzon* the lingual skeleton likewise consists of three segments, of which the anterior comprises four pieces whereas the others are unpaired. The two foremost segments are quite short, situated in the "tongue", the hindmost is very long, forming the lingual cartilage ("piston lingual").

In the following table an attempt is made to compare the skulls of *Petromyzon, Myxine* and Gnathostomes according to the preceding discussion. Much of this comparison is very hypothetical and needs to be reinforced by further arguments before it can be fully accepted.

| Petromyzon | Myxine | Gnathostome |
|---|---|---|
| *Neural skull.* | | |
| Parachordals (posterior?) | Posterior parachordals | Posterior parachordals (in Ganoids and teleosts) |
| ——? | Lamina basiotica | Lamina basiotica |
| Trabecle | Trabecle | Trabecle + polar cartilage |

| Petromyzon | Myxine | Gnathostome |
|---|---|---|
| ——?— | Hypophysial cartilage | Cartilage in the polar fenestra (sharks and rays) |
| ——?— | Ethmoid commissure (Palatine bar) | —— |
| Trabecular commissure | Trabecular commissure (in embryo) | Trabecular commissure |
| Pedicle process | Preauditory transverse bridge | Basitrabecular process |
| Nasal capsule | Nasal capsule | Primary nasal capsule? (HOLMGREN, 1940) |
| —— | —— | Secondary nasal capsule |
| *Visceral skeleton.* | | |
| Base of extrahyal + subocular arch | Dorsal longitudinal bar with commissure | Antorbital process + lamina orbitonasalis (HOLMGREN, 1943) |
| —— | First internal branchial arch | First branchial arch |
| —— | Hyoid arch (rudimentary) in embryo | Hyoid arch |
| ? | Palato-quadrate in embryo (rudimentary in adult) | Palato-quadrate |
| ? | Toothplate cartilage | Mandibular complex (in Holocephalians and *Antiarchi*) (HOLMGREN, 1942) |
| Cornual cartilage[1] | ? | —— |
| —— | (Post)symphysial plate of the tooth plate | Mandibular symphysial cartilage |
| Medial ventral plate | ? | ? |
| Anterior lateral plate (premandibular arch?) | Labial cartilage | ? |
| Second external branchial arch | Second external branchial arch | Second lower extra-branchial |
| First external branchial arch | First external branchial arch | First lower extra-branchial |
| Extrahyal | External hyal arch (1st prebranchial arch) | Extra-hyal (upper) |
| Extra-mandibular (styliform cartilage) | Extra-mandibular (dorsal) | —— |
| Medial lingual (medial apicalis) | Medial frontal basal plate | Copulae of the hyobranchial skeleton (?) |
| Lateral lingual (lateral apicalis) | Lateral frontal basal plate | |
| Connecting piece of the apicales (unpaired) | Medium basal plates (paired in the adult, unpaired in the embryo) | |
| Unpaired lingual cartilage | Unpaired caudal basal plate | |
| Velar skeleton | Velar skeleton | —— |

[1] It seems possible that the cornual cartilage of *Petromyzon* may answer to the toothplate cartilage in *Myxine*.

| Petromyzon | Myxine | Gnathostome |
|---|---|---|
| *Buccal skeleton.* | | |
| Posterior dorsal plate | Subnasal cartilage | Prelabial cartilage (in *Holocephalians;* HOLMGREN, 1942) |
| Anterior dorsal plate | ? | Prenasal cartilage (in *Holocephalians*) |
| Posterior lateral plate | Cornual cartilage | Pedicle cartilage (in *Holocephalians*) |
| Annular cartilage | ——— | Premaxillary cartilage (in *Holocephalians*) |
| Stylet cartilage | ——— | ——— |
| ——— | ——— | Labial cartilages |

## 9. THE MUSCLE RUDIMENTS OF THE HEAD OF THE EMBRYO.

SEWERTZOFF (1916) has stated that in the young larva of *Petromyzon* the musculature of the head is arranged in groups with a segmental appearance. These groups are: 1. The anterior buccalis group with the mm. buccalis anterior externus and internus. 2. The posterior buccalis group with the mm. buccalis posterior superficialis and profundus. 3. The velaris group with the m. constrictor velaris and the mm. velares profundi. 4. The extrahyal group with the m. constrictor prebranchialis I and the later developing m. adductor prebranchialis I. 5. The first branchialis group with the m. constrictor and the later appearing m. adductor branchialis I. Nos. 1 and 2 are innervated by the ramus maxillaris $V_2$, No. 3 by the ramus mandibularis $V_2$, No. 4 by ramus hyomandibularis VII and No. 5 by the ramus branchialis IX (first constrictor and adductor).

SEWERTZOFF (1923) and others found some of these groups represented in Gnathostomian fishes. The two foremost (1. and 2.) are missing there, and the third group is represented by the rudiments of the mandibular muscles (m. levator maxillae, adductor mandibulae and levator labii superioris). Otherwise the conditions are principally as in *Petromyzon.*

In my younger *Myxine* embryo the development of the visceral musculature is so far advanced that it is possible to make out the essentials of its components. In the head the muscles are arranged in groups as in the larva of *Petromyzon.* The groups being: 1. The buccalis group, 2. the velar group, 3. the hyoid and 4. the first branchial muscle plate. 5. a longitudinal muscle rudiment associated with the posterior and middle pieces of the basal skeleton, and 6. the muscle rudiments of the "pharyngeal roll". The first four of these rudiments correspond to the second to fifth in *Petromyzon.*

1. The buccalis group in the *Myxine* embryo consists of two muscle plates, one deep (m. buccalis profundus) (figs 14, 28 *m.b.p.*) and one superficial

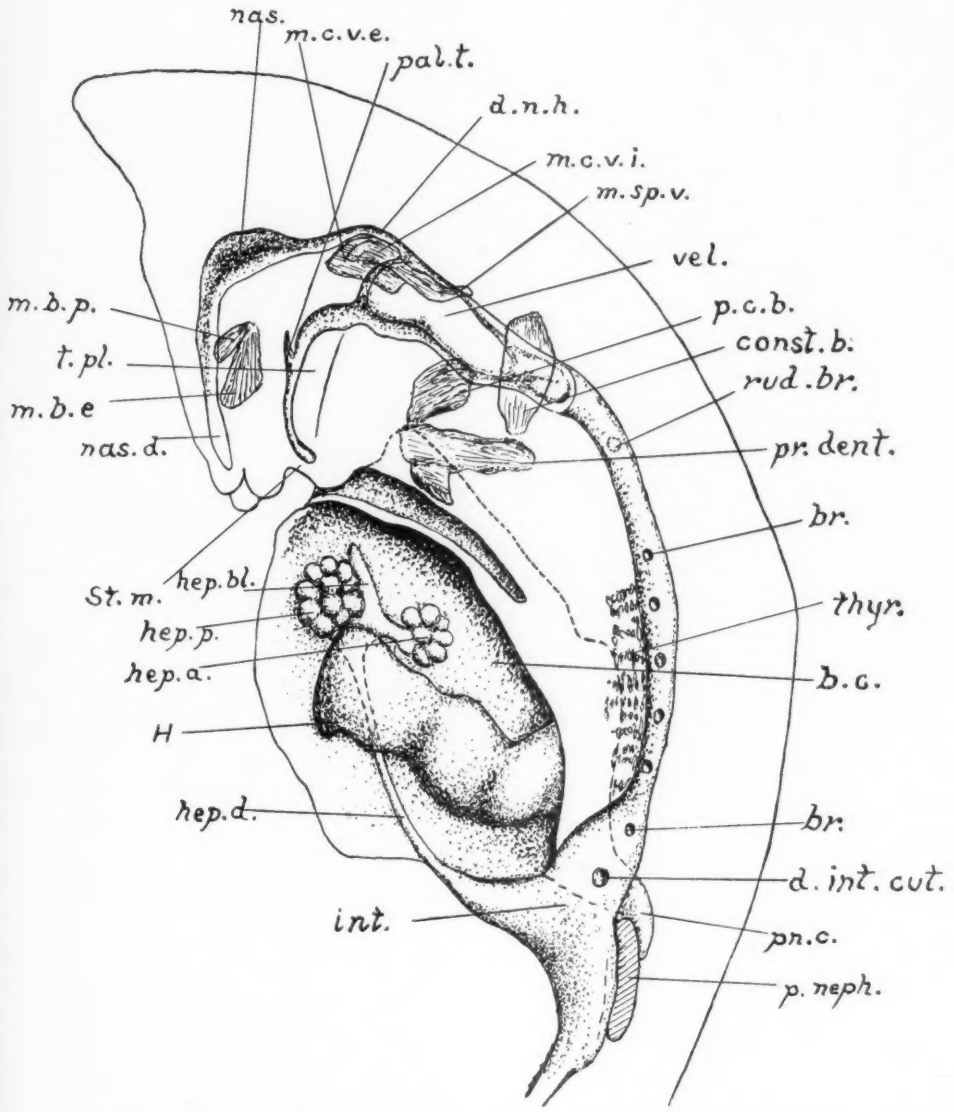


Fig. 28. Reconstruction from serial sections of the anterior part of the embryo, to show the segmental muscles, the velum, the intestine, the body-cavity, with heart and liver. 31 ×.

(m. buccalis superficialis) (figs 14, 28 *m.b.e.*). Both seem to be inserted into the fronto-lateral part of the palatine bar at the base of the cornual cartilage. The buccalis profundus extends fronto-mediad and ends in part laterally to the nasal canal, in part connected with the subnasal cartilage. The buccalis superficialis, which is much longer and broader than the profundus, extends

towards the tentacular portion of the face nearly parallel to the nasal canal. In the adult these rudiments may correspond to the entire maxillaris-innervated musculature in the anterior region of the head.

2. The velar group likewise consists of two muscle rudiments (figs 19—23, 28), the mm. craniovelaris externus (*m.c.v.e.*) and internus (*m.c.v.i.*). Both are, like the velum, disposed longitudinally. Both begin at some distance in front of the velum below the naso-pharyngeal duct on a level with the hypophysial commissure, and enter the velum. Both are inserted into the club-shaped frontal portion of the velar cartilage, but the internus continues behind its insertion point and leaves the velar fold in a caudo-medial direction. This part of the muscle probably represents the future m. spino-velaris. The m. cranio-velaris externus is a short but very strong, cylindrical muscle; the internus forms a more or less horizontally disposed, strong muscle-plate. The m. spino-velaris is rather weak. The velar muscles are innervated by the mandibular nerve (in the adult). The externus probably corresponds to the m. constrictor velaris and the internus to the mm. velares profundi in *Petromyzon*.

3. The hyoid muscle plate is a triangular lamella (fig. 28 *p.c.b.*) lying in front of the first extra-branchial arch and laterally to the dorsal part of the medium portion of the basal skeleton. Dorsally the plate reaches up laterally to the ventral branchial bar. This muscular plate is split up into a weak dorsal portion and a strong ventral one. The plate will probably develop into the m. protractor cartilaginis basalis (anterior and posterior) and perhaps also the m. cranio-hyoideus, both of which are innervated by the facial nerve. It may be pointed out that the muscle plate does not cover the extrabranchial arches but covers a part of the inner branchial system on its outside.

4. The first branchial muscle plate or m. constrictor branchialis I (figs 26—28 *const.b.*) lies behind the extrabranchial arches and externally to the first inner branchial arch. The muscle is dorsally bent strongly inwards so as to cover the upper end of the branchial arch. The glosso-pharyngeal nerve pierces the upper portion of the plate to innervate it from its inside. This branchial muscle is certainly homologous with the m. constrictor branchialis I. of *Petromyzon*.

5. The longitudinal muscle rudiment is the rudiment of the m. protractor dentium of the adult. In the embryo this rudiment (figs 20—28 *pr.dent.*) still has no connection with the dental plate, but its anterior end is directed towards the anterior part of this plate. It lies laterally to the medium and to the frontal parts of the posterior section of the basal skeleton. Its frontal end is on a level with the lower border of the anterior portion of the basal skeleton. As this muscle later becomes inserted into the anterior border of the dental plate and this plate moves caudad, the tendon of the muscle will slide over the frontal border of the basal skeleton, as it does in the adult animal. The protractor dentium is a strong muscle rudiment. Frontally it is connected



VOL
27
194

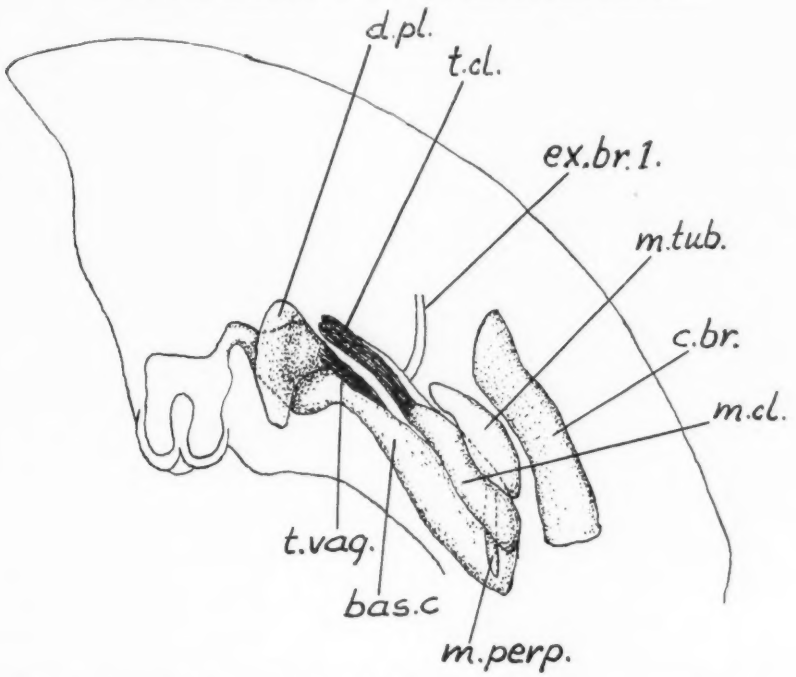


Fig. 29. Reconstruction from serial sections of the pharyngeal roll muscles. 31 ×.

with its vis-à-vis by a thin muscular lamella, running ventrally to the basal skeleton. In the adult the protractor muscle of the dental plate is innervated by the mandibular nerve and the same is probably the case in the embryo.

6. The muscle rudiments of the "pharyngeal roll" are already so far developed that it is possible to identify them with certainty. They are the m. tubulatus, clavatus and perpendicularis (fig. 29). But the disposition of these muscles is somewhat different compared with that of the adult. In the adult the clavatus, except for its anterior and posterior parts, is entirely surrounded by the tubulatus. The clavatus is inserted into the dental plate by means of a long and strong tendon. The muscle is paired, but its tendon is unpaired with the exception of its anterior end, which is cleft into two strong branches, the point of insertion lying somewhat laterally on the dental plate. The tendon is surrounded by a scattered connective tissue, and externally to this a strong layer of collagenous fibres forms a sheath surrounding the tendon. This sheath with the tendon lies in a wide blood sinus belonging to the medial ventral jugular vein, into which the tendon with its sheath is able to move backwards and forwards. The sheath of the tendon gradually thickens frontally in the ventral midline towards the dental plate, into which this thickened part is inserted as a very strong tendon. The point of insertion lies quite medially on the dental plate. Thus in the "tendon" of the clavatus

muscle of the adult there are present two different structures, viz. the tendon of the clavatus muscle and that of the vaginal sheath.

The essentials of these structures are present in the embryo, but the "tendon" is still not separated from the surrounding tissue as the blood sinus has not yet developed, but a rich system of capillaries surround the space where the "tendon" is developing. These capillaries probably represent the future blood sinus. The blood of these capillaries runs into the medial ventral jugular vein. The two real tendons are already indicated (fig. 29 *t.cl.*, *t.vag.*) in the rudiment of the "tendon". The dorsal one, which caudally connects up with the clavatus muscles, is frontally cleft but is not yet inserted into the dental plate. The ventral (*t. vag.*) is also present, bring inserted into the mid-ventral line of the plate.

The m. clavatus is paired (figs 26, 27, 29 *m. cl.*), the two muscles being separated by a broad mesenchymatic septum. Caudally the muscles end in a dense mesenchyme with diffuse borders. This mesenchyme is probably the rudiment of the superior and inferior chondroid bars of AYERS and JACKSON (1900). These bars are not yet differentiated.

The tubulatus muscle of the embryo is likewise paired (figs 26, 27, 29 *m.tub.*). It is situated dorso-laterally to the clavatus. Frontally the rudiments begin on a level with the anterior end of the clavatus muscle. The frontal end is embedded in a rather dense mesenchyme. The muscle forms a somewhat flattened mass of which the medial border partly reaches near to the medial line, whereas its lateral borders, partly at least, cover the clavatus muscle mass. Caudally the muscle ends in the same mesenchyme as the clavatus. The tubulatus of the embryo displays no tendency to become tube-like.

The m. perpendicularis (fig. 29 *m.perp.*) is also present. Its dorsal as well as its ventral end is connected with the mesenchyme of the chondroid bars.

In the space between the constrictor branchialis I and the first branchial sac a long constrictor branchialis (fig. 29 *c.br.*) plate is developed. This plate is probably composed of smaller constrictors belonging to branchial sacs which have been reduced. (It may be pointed out that a rudimentary gill pouch is present in this space.)

In view of the fact that not a single one of the muscles in *Myxine* could with any degree of certainty be homologized with any muscle in *Petromyzon*, it is of considerable interest to note that the muscle groups of *Petromyzon* could be shown to be present in *Myxine*. This furnishes us with a reliable basis for further comparisons.

## 10. THE SKIN.

The skin of my *Myxine* embryos consists of two epithelial layers, a basal membrane (corium) and a mesenchymatous subdermal layer.

The external layer of the epithelium contains somewhat irregular cells with rather small nuclei. The basal parts of these cells are wedged in between the cells of the internal layer. The cells of the latter are mostly broad cylindrical with a relatively large rounded nucleus, but narrow cylindrical cells are also present. The internal layer rests upon a very thin collagenous basal membrane or connective tissue lamella (corium). Internally to this lamella follows a fairly dense mesenchyma, of which the external cells, especially in the dorsal part of the embryo (fig. 30 *m.l.1.*), are arranged as an indistinctly epithelium-like layer with somewhat larger nuclei. Inside this layer the nuclei are smaller (fig. 30 *m.l.2.*) and the cells more irregularly arranged. Those bordering on the epithelium-like layer are often flattened against it. The deepest part of the mesenchymatic layer (fig. 30 *m.l.3.*) consists of more scattered cells forming a mesenchymatic network.

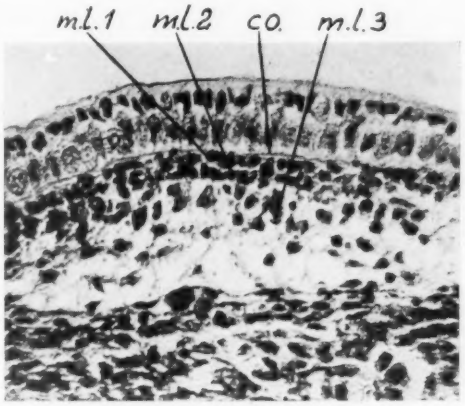


Fig. 30. Transversal section through the skin of *Myxine* embryo.

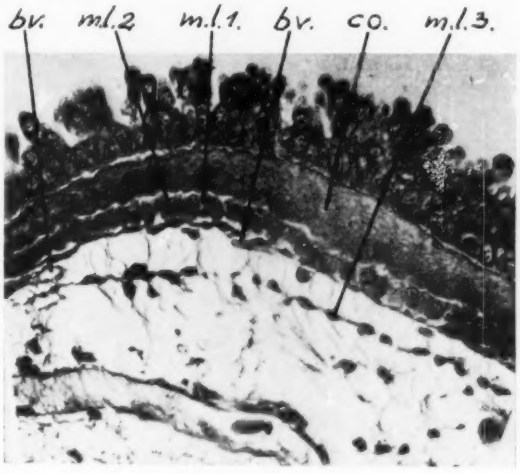


Fig. 31. Transversal section through the skin of a *Myxine*, 43 mm long.

In my 43-mm specimen the skin is much more highly developed, though not more than that the embryonic parts could be recognized without difficulty. The epithelium is now well differentiated with thread-cells and vesicular cells more or less as in the adult. The superficial cells do not form an uninterrupted layer, but the individual cells extends club-like above the general surface of the epithelium (fig. 31).

The basal membrane is replaced by a fairly thick collagenous, cell-free corium. Beneath the corium follows a mesodermal layer composed of broad cylindrical cells, which are arranged as a simple epithelium in such a manner that it could be mistaken for an epithelium, were it not situated inside the

corium. This layer is apparently the principal matrix layer of the corium. In sections in which the matrix has been somewhat torn away from the corium it is clearly seen that collagenous fibres from the external surface of the cells enter the corium, there forming part of its lamellae. In my sections the nature of the corium could not be investigated in detail, the state of preservation not being sufficient for this purpose. Here are, however, indications that it is in the nature of an aponeurosis. The deep surface of the epithelium-like layer is covered by a simple endothelium-like layer of flattened, scale-like mesenchyme cells. These border upon a broad space with scattered cells, but with a large number of collagenous fibres traversing it. Fibres from this layer traverse the epithelium-like layer and enter the corium, where they apparently take some part in forming this layer. Capillaries are collected on the inner surface of the epithelium-like layer but do not enter it. In this space with scattered cells cell laminas are often met with (fig. 31 *m.l.3.*), consisting of connected flat mesenchymatic cells, sending fibres perpendicularly to the corium.

The skin of a 100 mm and of larger specimens has a thick corium forming the well-known aponeurosis. It consists of two layers, an outer and an inner. The outer layer is composed of thin collagenous bundles aponeurotically arranged in three, four or five layers. This part of the corium contains no cells. It may be pierced by narrow perpendicular blood vessels which enter the epithelium. It is separated from the underlying part of the corium by more or less tangentially arranged, mostly pigmented blood capillaries, from which the already mentioned perpendicular vessels issue. The internal part of the corium is also composed of collagenous bundles, but these bundles are much stronger than those of the external layer. They also form a regularly composed aponeurosis. But this aponeurosis differs from that of the external part of the corium as it contains cells scattered over the collagenous bundles. Their nuclei are flattened between the bundles forming rather long ovoid bodies, extended in the direction of the bundles. The internal layer is delimited from the subdermal connective tissue by means of a thin layer of flattened cells with elongated nuclei. These cells are very sharply outlined and contain a strongly refractive matter, which is apparently the initial stage of a collagenous bundle. This matter is especially concentrated at the internal surface of the cells, whereas the external part of the cells, especially on the dorsal side of the animal, sometimes contains masses of pigment corpuscles. This cell layer must be regarded as a matrix layer for at least one lamella of the aponeurosis. Below this layer there may be another layer of similar connective tissue cells, which, however, do not contain the refractive substance. These are probably cells which will later form a new matrix. The growth of the corium is effected through apposition of the matrix cells, with their thickening collagenous bundles, to the internal surface of the corium. The cells are thereby embedded



VOL.
27
194

in the corium successively, as new cells from the subdermal connective tissue replace the embedded cells. The pigment has now disappeared. Comparing the skin of the 100-mm specimen with that of the 43-mm, we thus find the following differences.

1. In the 100-mm specimen the corium is composed of two different layers, the external cell-free, the internal with cells. In the 43-mm specimen but one cell-free layer is present.

2. In the 43-mm specimen the lower surface of the corium is covered with a layer of epithelium-like cells. In the 100-mm specimen no traces of such cells are found.

3. Internal to the epithelium-like cells is an endothelium-like layer in the 43-mm specimen. In the 100-mm specimen such cells cover the internal surface of the corium and are successively embedded in the corium forming with their collagenous bundles the internal cellulated part of the corium. It is easy to imagine that in an initial stage of formation of this part there was a single layer of such endothelium-like cells, which transformed into a layer of the future aponeurosis, and thus became embedded in it. A new layer of matrix cells was then formed, and so forth. I conclude from the preceding statements that the endothelium-like layer in the 43-mm specimen represent the original matrix cells of the internal layer of the corium. The preceding statements seem to admit of following conclusions.

1. The epithelium-like cells are the matrix cells of the external cell-free part of the corium in the adult *Myxine*. 2. These cells disappear after they have produced this part of the corium. 3. The endothelium-like layer in the 43-mm specimen is the matrix of the first forming layer of the internal cellulated part of the corium. The cell-lamina seen in the subdermal connective tissue in the 43-mm specimen may represent a layer of future matrix cells, which might later be added to the corium.

## II. THE BRAIN.

The development of the brain of *Myxine* is completely unknown. But as some researches have been made in the brain development of *Bdellostoma* our lack of knowledge concerning *Myxine* is not very important, the two genera being very similarly built regarding this part.

Our knowledge of the development of the brain in *Bdellostoma* is based upon the researches of KUPFFER (1892, 1906) and of CONEL (1929, 1931). The latter in particular had a comparatively large body of material at his disposal. But this material does not seem to have been well preserved, so that its usefulness has been limited. The same is the case with my two *Myxine* embryos. Nevertheless they have yielded some results worth mentioning. In

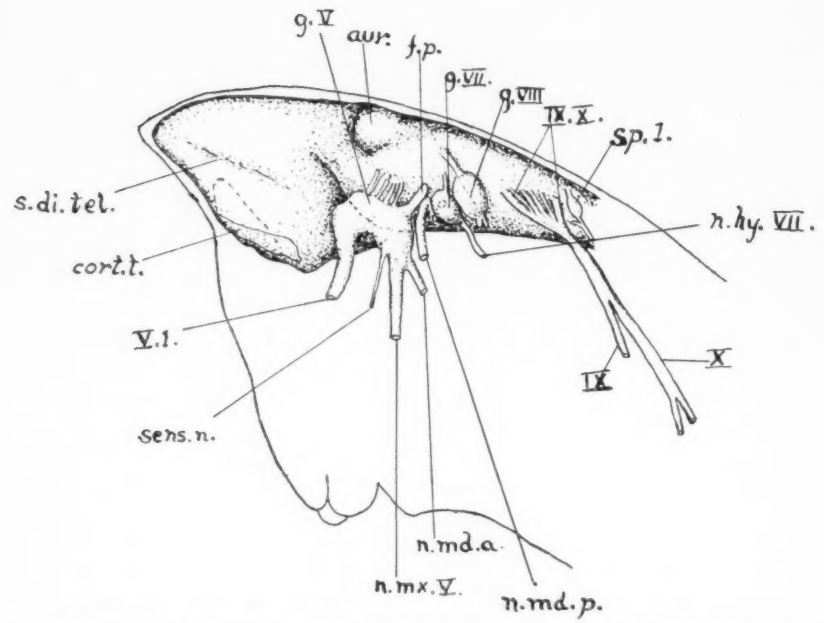


Fig. 32. Reconstruction from serial sections of the brain of *Myxine* embryo, lateral aspect. *g.VII*, utricular ganglion; *g.VIII*, saccular ganglion. 31 ×.

the following remarks I will only use the younger of the two embryos, as it is better preserved than the other though far from well preserved. Its brain is, however, slightly depressed; otherwise it seems to have preserved its principal characters. I will now give a description of it.

## A. LATERAL ASPECT.

As mentioned in the preceding pages, the dorsal surface of the frontal end of the embryo forms a cephalic shield. Immediately inside this shield lies the brain. Frontally it extends into the frontal marginal portion of the shield. From this foremost point the brain outline turns in a caudo-ventral direction, following the frontal surface of the head to meet the olfactory sac ventrally. There, the outline turns caudad, forming a convex line which ends in the posterior margin of the infundibulum, which overlaps the brain flexure. At about the middle of this convex line lies the exit of the optic nerves. The brain flexure is very deep and extends in a fronto-dorsal direction. The olfactory nerves are very short and enter the nasal sac immediately. Thus the bulbar formation is directed ventrad. On the lateral side of the frontal brain portion is seen an obliquely located long groove (fig. 32 *s.di.tel.*), which roughly marks the boundary between the telencephalon and the tweenbrain.

The boundary between the premedullary part of the brain and the medulla oblongata is marked from the lateral aspect by the somewhat protruding auricular lobes of the rhombencephalon. From a lateral view the brain of my *Myxine* embryo recalls that of the *Bdellostoma* embryo No. 7 and 17 (of CONEL), but the external features are less marked. No. 7 corresponds to DEAN's figure 45 of *Bdellostoma* embryos, in which there are still 4 gill-slits lying on the yolk and where the embryo has not yet reached the anterior and posterior ends of the surface of the egg. Fig. No. 17 corresponds approximately to DEAN's figure 47, in which the head of the embryo has reached the anterior egg-pole but the tail has not yet reached the posterior pole.

## B. DORSAL ASPECT.

In this view the brain consists of two portions of which the posterior is the medulla oblongata, the anterior the rest of the brain, comprising the telen-, dien-, mesencephalon and perhaps also the cerebellum. The anterior part is considerably broader than long, connected with the oblongata by means of the broad cylindrical mesencephalic portion (*mes.*). The medulla oblongata is frontally very broad, not very much narrower than the anterior brain portion. It narrows caudad by degrees. In the midline the anterior portion has two large "fontanellae" (fig. 33 *font.* 1 and 2), i.e. portions where the ventricular system is covered with ependyme only. The anterior of these "fontanellae" extends from near the anterior pole to near the middle of the anterior brain portion. It forms an equilateral triangle with the base caudad. The posterior "fontanella" extends over the caudal third. It is comparatively narrow but sud-

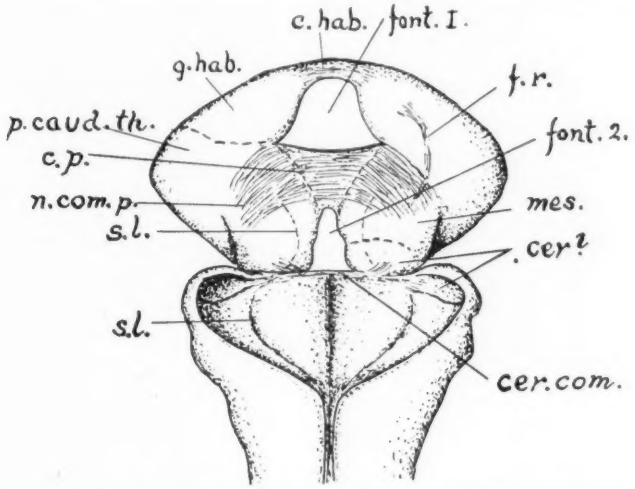


Fig. 33. Reconstruction from serial sections of the brain of *Myxine* embryo, dorsal aspect. 31 ×.

denly widens caudally in front of the auricular lobes of the medulla oblongata. Between the two fontanellae is a broad commissural lamina (posterior commissure) (*c.p.*). The fossa rhomboidalis of the medulla oblongata is very broadly triangular, being separated from the posterior fontanella of the anterior brain portion by a narrow but rather strong commissural bar (*cer.com.*). The fossa rhomboidalis is continued caudally by a narrow fissure (covered with epithelium) extending caudad in the dorsal midline of the spinal cord.

As the reconstructions published by CONEL do not indicate the presence of "fontanellae" and his microphotographs do not either give any idea of the occurrence of ependymal membranes covering any fontanellae, I must assume that they were not very conspicuous in *Bdellostoma* embryos and had not a degree of development corresponding to that of my *Myxine* embryo. On the other hand, my embryo displays no external sulci, except for the di-telencephalic. It is not possible therefore to make a detailed comparison with CONEL's *Bdellostoma* stages. My *Myxine* brain seems, however, to agree more closely with CONEL's specimen 17 than with his specimen 7.

## C. VENTRAL ASPECT.

The anterior part of the brain as seen from the ventral side has the same outlines as it has in its dorsal aspect with the difference, however, that the caudal part is drawn out into a broad triangular obtuse hypothalmic lobe, below the posterior pole of which is placed the transversely lying hypophysial rudiment (*hyp.*). The epithelial lamina terminalis (*l.t.*) is seen in the midline as a narrow strip widening frontally and caudally. They widened anterior part is sunken in to form a rather deep fossa (*v.tr.*?). The lamina terminalis extends from near the frontal margin to the posterior third of the anterior brain portion. A short distance behind the posterior border of the lamina the eye-nerves (*II*) are visible.

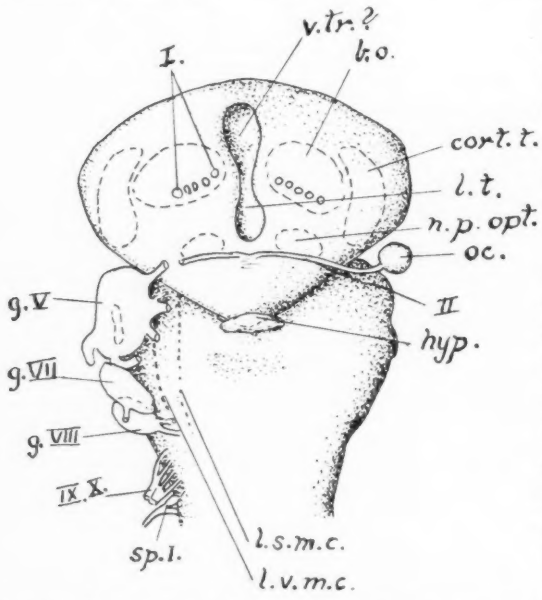


Fig. 34. Reconstruction from serial sections of the brain of *Myxine* embryo, ventral aspect. *g.VII*, ganglion utriculare; *g.VIII*, ganglion sacculare. 31 ×.

The olfactory nerves issue from about the middle of the brain part on a line located from in front medially to caudad and laterad. No distinct mamillary lobes are seen on the hypothalamic part.

The ventral view of my *Myxine* brain has some points of agreement with that of CONEL's embryo No. 17, less with his No. 7.

## D. THE SAGITTAL SECTION.

The nervous parts of the sagittal section are: frontally the habenular commissure (fig. 35 *c.hab.*), dorsally the posterior (*c.p.*) and the cerebellar commissure (*com.c.*), ventrally the commissures of the chiasmatic ridge: chiasma and postoptic commissures. The caudal (dorsal) wall of the posterior tubercle and the ventral wall of the medulla oblongata contain masses of crossing or commissural fibres. The habenular commissure is very strong. The posterior commissure forms a rather thin but long and broad fibre layer crossing over the midline. The cerebellar commissure is very long bot not very strong, lying in the anterior wall portion of a transversal fold separating the anterior brain portion from the posterior (medulla oblongata). The chiasma ridge is rather thick, frontally delimited by a shallow pocket, the preoptic recess, and caudally passing by degrees into the ventral wall of the hypothalmus. The lamina between the preoptic recess and the habenular commissure would normally be occupied by the lamina terminalis (fig. 35 *l.t.*), the recessus neuroporicus (fig. 36 *n.por.?*), the lamina supraneuroporica, the velum transversum (fig. 36 *v.tr.?*) and the dorsal sac. In my *Myxine* embryo these parts cannot be differentiated with any certainty. In *Bdellostoma* the position of these parts is problematic, as they have been located rather differently at the different stages of development. For instance, the recessus neuroporicus

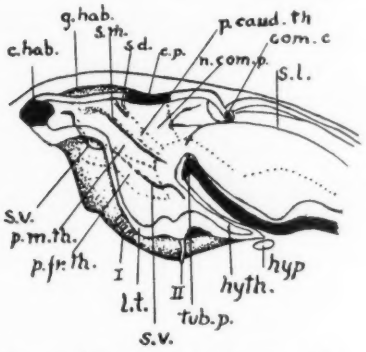


Fig. 35. Reconstruction from serial sections of the brain of *Myxine* embryo, inside aspect, with brain areas outlined. 31 ×.

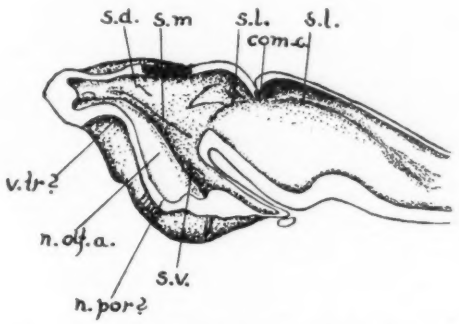


Fig. 36. Reconstruction from serial sections of the brain of *Myxine* embryo, inside aspect. 31 ×.

of embryos No. 7 and 17, lying behind a long lamina supraneuroporica, can scarcely be the same as that of the embryo 2270, in which it lies immediately in front of the habenular commissure, the lamina supraneuroporica being absent[1]. The velum transversum[2] in embryos No. 9 and 7 lying at the frontal end of the brain at the place of the habenular commissure cannot be a velum transversum. The dorsal sac of the *Bdellostoma* embryos situated behind the habenular commissure and in front of the epiphysis is no dorsal sac, comparable with that in other fishes. The identification of these parts therefore seems to be rather doubtful. In the sagittal section of my *Myxine* embryo a rounded pocket at some distance in front of the chiasma ridge may possibly represent the recessus neuroporicus, and an infolding in front of (below) the habenular commissure may be the velum transversum. In the latter case the dorsal lamina of the fold would contain the true dorsal sac. But these suggestions are as problematic as those of CONEL regarding his *Bdellostoma* embryos. Moreover, the dorsal commissures offer difficulties compared with the different stages of *Bdellostoma*. In CONEL's stage No. 9 the fissura di-mesencephalica is placed far away from the habenula (CONEL's fig. 36), at a place answering to the boundary between the "mesencephalon" and the medulla oblongata, where in his fig. 10 (CONEL, 1929) the fissura rhombo-mesencephalica is located. The thickening in the roof of this place in fig. 36 does not represent the position of the commissura posterior but of the commissura cerebellaris. The location of the true commissura posterior of this stage is uncertain but ought to be somewhat behind the habenular ganglion. In embryo No. 7 the commissura posterior is also placed as in embryo No. 9 and must likewise be the cerebellar commissure, the commissura posterior not being recognized, but the fissura rhombo-mesencephalica lies in about the same position as in the preceding stage and in the same relation to the sulcus isthmi and the tuberculum posterius (Compare my fig. 36 of *Myxine*). The location of the posterior commissure is not indicated. In No. 2270 the posterior commissure, according to fig. 108 compared with 91, must lie immediately behind the "epiphysis" in the brain portion indicated as the pars intercalaris diencephali. In No. 2266 the posterior commissure lies in the "pars intercalaris diencephali" a considerable distance behind the "epiphysis" and behind the "dorsal sac". There is a considerable distance between the commissura posterior and the commissura cerebellaris. In No. 2267 fig. 124 compared with the sections 132, 133 and 134 the commissura posterior lies immediately behind the "epiphysis" and far in front of the cerebellar commissure. No. 1 behaves as No. 2267, but the plica rhombo-mesencephalica is solid, indicating perhaps a stronger commissura cerebellaris

[1] According to CONEL (1931) the recessus neuroporicus can be identified only in the embryos Nos. 9 and 11, but in the figures it is also indicated in figs of Nos. 7, 17 and 2270.

[2] CONEL (1931) identifies the velum transversum only in 9, 11 and 7. It may, however, be the ridge in which the habenular commissure will appear.

than in the preceding stage. In my second *Myxine* embryo, which is somewhat older than the embryo used for my descriptions, the commissure is much stronger than in the latter.

## E. THE VENTRICULAR WALL.

*The telencephalon.*

My *Myxine* embryo is already so far advanced that some distinct cellular areas are recognizable at the ventricular wall. Thus many nervecells have emigrated from the ventricular layer. The emigration has not taken place uniformly along the entire ventricular wall, there being areas with few emigrated cells and areas with a greater number. It is thus that the mentioned cellular areas arise. In some of these areas the emigration has apparently proceeded in stages so that special nuclei have been formed outside the ventricular layer of ganglionic cells. Two such nuclei are seen ventrally (frontally) in the anterior brain portion. The one of these nuclei lies more medially than the other. As the olfactory nerves enter this latter nucleus (figs 40, 41 *b.o.*), it must be the bulbus formation. The ventricular cell layers underlying it must be the nucleus olfactorius anterior (figs 36, 40 *n.olf.a.*), which forms a great ventricular swelling on the ventral (frontal) ventricular wall, a swelling that in the longitudinally divided brain conceals from sight the lower (frontal) part of the lateral ventricular wall. The lateral part of this swelling also includes a part of the pallial portion of the forebrain (figs 34, 39—41 *cort.t.*). This pallial part lies laterally to the bulbus formation, outside the lateral part of the side ventricle (fig. 41). This nucleus forms a long cortex plate, which must be the first rudiment of the cerebral cortex, which is so strongly developed in the adult. The upper (caudal) boundary of the forebrain on the ventricular wall (fig. 35) extends to a line running from the preoptic recess caudally (ventrally), where there is an indistinctly characterized preoptic area (fig. 34 *n.p.opt.*), to the habenular commissure in front (dorsally). Frontally (dorsally) this line is curved upwards. On the lateral surface (fig. 37) of the brain the forebrain has a somewhat corresponding extension. It should be observed that

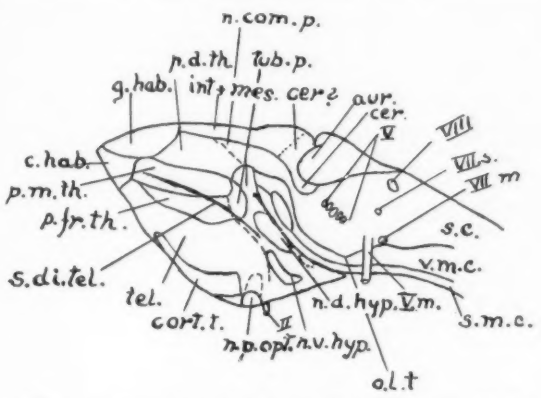


Fig. 37. Reconstruction from serial sections of the brain areas, outlined on the brain surface. *VII.s.*, root of the utriculare ganglion. 31 ×.

this lateral boundary line does not correspond to the long outside groove, interpreted by CONEL as the di-telencephalic boundary line (fig 37 *s.di.tel.*). In its main part the structural limit of the telencephalon lies considerably below (in front of) this groove. It seems certain, however, that in very young embryos the groove really signifies a di-telencephalic boundary line, but that it has lost this significance as the emigration of the ganglionic cells began and differentiation of the cell areas occurred. In my embryos the groove and the tractus olfacto-habenularis (figs 38, 39 *tr.olf.hab.*) follow one another so closely that it appears that the groove must be in some way dependent upon this tract. Inside it the ventricular layer has produced but few ganglionic cells, whereas the cell proliferation on each side of the tract is very active. Therefore the outer wall outside the tract may have sunken in, thus producing the outside sulcus.

*The diencephalon.*

Dorsally to the di-telencephalic boundary at the ventricular wall, as defined in the preceding lines, there follows a rather narrow area (figs 35, 38—41 *p.fr.th.*), extending from near the habenular commissure in front (dorsally) towards the lower (anterior) part of the tuberculum posterius. This area is not very clearly delimited caudally from a cell area surrounding the plica encephali ventralis. The thus delimited narrow area, which is located in a position about perpendicular to the longitudinal axis of the brain, contains a short ventricular groove situated in its posterior (ventral) part. This groove (*s.v.*) is probably a detached part of one which frontally (dorsally) runs along the dorsal (caudal) boundary line of the area. On the outside (fig. 37 *p.fr.th.*) of the brain this area is seen to occupy a field approximately corresponding to that of the ventricular wall, but it is here delimited from the tubercular area (*tub.p.*). The main part of the area, the inside as well as the outside part, lies below (frontally to) the di-telencephalic sulcus of CONEL. The area now under consideration is characterized by a vivid cell proliferation, so that only a thin layer of fibre is present on the outside of the cell masses. Dorsally (caudally) to the area described in the preceding lines there follows a similar narrow area (figs 35, 38—41 *p.m.th.*) extending from the habenular commissure and the anterior part of the rudiment of the habenular ganglion to the tuberculum posterius region, where it abuts on to this region (with determinable limits). A corresponding field is discernible (fig. 37 *p.m.th.*) on the outside. This area is characterized by a comparatively thin ventricular cell layer and by the rudiment of the tractus (olfactorius lateralis and) olfacto-habenularis (figs 38, 39 *tr.olf.hab.*) running outside the cell layers, i.e. through this area, on its way to the habenular commissure. Partly in this area, partly on its dorsal (caudal) boundary line runs a long sulcus (figs 35, 36, 39—41 *s.m.*), beginning in front below the rudiment of the habenular ganglion and



VOL
27
194

extending to the tuberculum posterius. In young stages of *Bdellostoma* the corresponding sulcus is a deep fissure, gradually becoming shallower in later stages of development.

Dorsally (caudally) to the preceding area there follows, at the ventricular wall, a new narrow area (figs 35 *p.caud.th.*, 40 *p.d.th.*). It begins frontally (dorsally) in contact with the posterior half of the rudiment of the habenular ganglion just in front of the commissura posterior. Its posterior (ventral) end merges without any visible boundary line into the region of the tuberculum posterius. Through this area runs the fasciculus retroflexus (tractus habenulo-peduncularis) (figs 33, 40, 41 *f.r.*) on its backward course to the interpeduncular nucleus. A short sulcus (figs 35, 36, 40, 41 *s.d.*) in its dorsal portion forms the dorsal (caudal) boundary of fasciculus retroflexus. On the outside this part of the brain is much more strongly developed (fig. 38 *p.d.th.*), so that it occupies there a rather broad field caudally (ventrally) delimited from the tuberculum posterius region.

The rudiment of the habenular ganglion (figs 33, 35, 37, 38, 39 *g.hab.*) has already been mentioned. It forms the thick upper border of the brain laterally to the frontal "fontanella" (fig. 33 *font.1*). Caudally it is delimited by the commissura posterior, which delimits the "anterior fontanella" likewise caudally.

Fig. 38. Transversal section through the anterior part of the head (section 31). 23 ×.

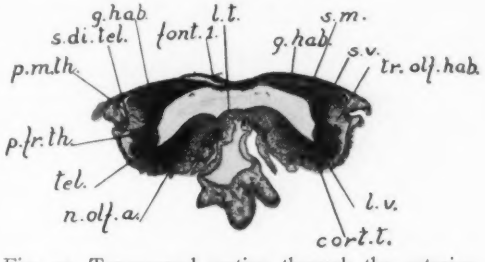


Fig. 39. Transversal section through the anterior part of the head, some sections behind fig. 38 (section 38). 23 ×.

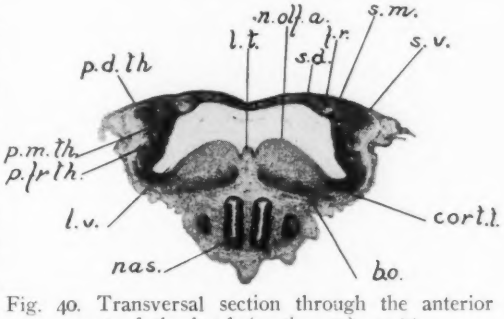


Fig. 40. Transversal section through the anterior part of the head (section 51). 23 ×.

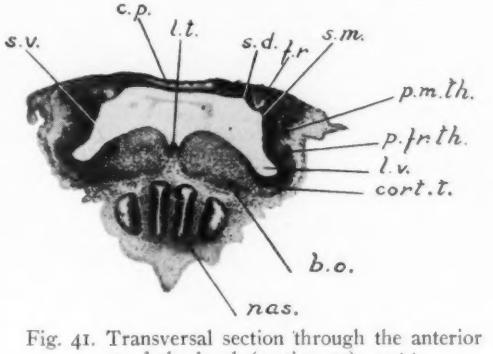


Fig. 41. Transversal section through the anterior part of the head (section 54). 23 ×.

The region of the tuberculum posterius is indistinctly delimited on the ventricular surface, as already mentioned. On the outside its limits are better defined. Ventrolaterally the regio tuberculi posterioris contains a specially differentiated superficial nucleus, consisting of densely crowded ganglionic cells. This nucleus corresponds to the nucleus tuberculi posterioris described by JANSEN (1930) in the adult brain. This nucleus of the adult is thus only a part of the region of the posterior tubercle. Ventrally the region of the tuberculum posterius of the embryo is in contact with the slightly developed nucleus dorsalis hypothalami. A nucleus ventralis hypothalami is also present, but no mammillary body could be determined with any certainty.

A comparison with other vertebrates will immediately reveal the significance of the diencephalic areas described in the preceding pages. In *Petromyzon* and all lower vertebrate embryos three distinct thalamic areas have been recognized (BERGQUIST, 1932). These form three parallel bandlike areas extending between the epithalmic part of the 'tweenbrain and the region of the tuberculum posterius. These parts are the *pars frontalis, medialis* and *caudalis thalami* respectively. In the pars frontalis runs the sulcus ventralis, in the pars medialis the sulcus medius and in the pars caudalis the sulcus dorsalis. These sulci may be placed somewhat differently in their areas. As they are so-called proliferation sulci (BERGQUIST, 1932), they invariably lie in the middle of their areas in very young embryos, but in older ones the position of the sulci in the areas can be variable or the sulci can be missing altogether. In *Amia* 8 mm the sulcus medius lies at the posterior border of its area. The sulcus dorsalis in *Petromyzon* and in *Myxine* lies caudally to the fasciculus retroflexus, in most other fishes frontally to it.

If we now compare *Petromyzon* with *Myxine,* the conditions of the thalamus of the latter are accurately the same as in *Petromyzon* with three parallel thalamic areas, each with its sulcus and extending from the habenular region to the tuberculum posterius. As it is highly improbable that the areas in *Myxine* differ from those in *Petromyzon,* they are in *Myxine:* the frontal, the medial and the caudal areas.

Thanks to CONEL's (1931) investigations on *Bdellostoma* we can easily foresee the subsequent developments in these areas: The frontal area will develop the great "*primordium hippocampi*", the medial the "*eminentia thalami*" and the "*nucleus ventralis thalami*" and the caudal the "*nucleus dorsalis thalami*".

Already in 1919, p. 13, footnote, I had some doubt about the identification of the "Thalamuskern" (EDINGER) with the telencephalic primordium hippocampi: "Ich werde den 'Thalamuskern' im folgenden als Primordium hippocampi bezeichnen. Ich betone aber, dass diese Bezeichnung auf der Voraussetzung ruht, dass, was bei *Petromyzon* früher als Praethalamus beschrieben wurde, wie JOHNSTON bewiesen zu haben scheint, dem Primordium hippocampi entspricht. Künftige Untersuchungen werden diese Auffassung JOHNSTON's

bestätigen oder verwerfen. Im letzteren Fall wird es für *Myxine* nötig werden, die eingeführte Bezeichnung (Prim. hipp.) mit einer anderen auszutauschen." In 1922 I identified the primordium hippocampi of JOHNSTON with the eminentia thalami in Amphibians. This conclusion was accepted by KUHLENBECK (1929) and by JEENER (1930), but the definitive statement of the correctness of my conclusion is found in BERGQUIST's work (1932), in which he has followed the development of the thalamus in representatives of the different groups of anamnian vertebrates. Where, as in most fishes, the pars frontalis thalami differentiates, it forms the nucleus ventralis thalami. The pars medialis thalami gives rise to the eminentia thalami and the nucleus medialis thalami. The pars caudalis thalami either remains undifferentiated or forms the nucleus dorsalis thalami as essential nucleus.

In the preceding lines I have traced the caudal boundary of the diencephalon from its lateral aspect. In fig. 33 I have reconstructed the boundaries of the cell territories on the dorsal surface of the anterior brain portion. In this figure it is clearly seen that the pars caudalis diencephali (nucleus dorsalis thalami) (*n. caud.th.*) abuts frontally on to the habenular area. Medially it is shut off from the medial line by the synencephalon, which frontally reaches the posterior border of the habenular area and in which the frontal part is occupied by the broad commissura posterior. The synencephalon of KUPPFER forms the third segment of the diencephalon (PALMGREN, 1921). It contains the posterior commissure, which, however, is generally regarded as part of the mesencephalon. It closely corresponds to the pars intercalaris diencephali of HERRICK. According to BERGQUIST, who has also studied the development of this part of the brain, the intercalar nucleus, the dorsal part of the synencephalon, is the regio commissurae posterioris and the ventral part the nucleus fasciculi longitudinalis, the regio thus generally forming a band of cells in front of the mesencephalic segments. The same may also be the case in *Myxine*, but the posterior border of the region could not be traced with any certainty, except for its commissural plate. The *commissura posterior passes over the dorsal surface of the intercalar region*, and this must also have been the case in *Bdellostoma*. There the intercalar part decreases in length and width with increasing age. Dorsally it always lies immediately behind the "epiphysis", and in later stages immediately behind the habenular ganglia. As the intercalar region contains the commissura posterior, the latter must be located immediately behind the habenular ganglion. It does not therefore seem to be theoretically impossible that, in the adult at least, part of the commissural fibres can be embedded in the habenular ganglion, especially if the intercalar part becomes partly overgrown by the increasing dorsal thalamus.

In the *Myxine* embryo the fibres of the posterior commissure (fig. 33 *c.p.*) could be followed for some distance laterad. After they have passed the commissural plate they turn caudo-laterad and could be followed to the antero-

lateral part of the mesencephalon. They thus pass through a cell area which may perhaps represent the nucleus intercalaris and more ventrally the nucleus commissurae posterioris, which, however, is not differentiated. If we apply BERGQUIST's result to the conditions in *Myxine*, the following conclusions must be drawn:

1. The "primordium hippocampi" of earlier writers on Myxinoids is the *nucleus ventralis thalami* (belonging to the pars frontalis thalami) and has nothing to do with the real primordium hippocampi, which is a telencephalic part.

2. The "*nucleus ventralis thalami*" of earlier researchers seems to correspond almost exactly to the *nucleus medialis thalami* (of BERGQUIST) and that of the *Myxine* embryo.

3. The *eminentia thalami* constitute the dorsal part of the pars medialis thalami, of which the nucleus medialis thalami is the ventral. It answers to the eminentia thalami in Amphibians and *Petromyzon* (BERGQUIST).

4. The *nucleus dorsalis thalami* is part of the *pars caudalis thalami*, which corresponds to the intercalar nucleus of HERRICK, situated in front of the posterior commissure in *Necturus*.

5. There is no specific intercalar part in the sense of HERRICK present in the *Myxine* embryo, this part being there the pars caudalis thalami of BERGQUIST.

6. The pars intercalaris diencephali of CONEL seems to correspond to the commissural plate of the posterior commissure and thus belongs to the dorsal part of the regio commissurae posterioris of BERGQUIST. In *Necturus* this regio lies behind the intercalar part of HERRICK, which corresponds to the dorsal part of the pars caudalis thalami of BERGQUIST (= pars dorsalis thalami of CONEL).

*The mesencephalon and the cerebellum* (figs 33—37).

The commissura posterior belongs genetically to a special brain segment — the synencephalon of KUPFFER — which is generally considerated to be a part of the mesencephalon, a conception, which I will use here.

The anterior limit of the mesencephalon is well determined through the posterior boundary line of the pars caudalis diencephali, which is the nucleus dorsalis thalami (according to BERGQUIST) or the intercalar nucleus (according to HERRICK). The posterior limit is very difficult to trace owing to the interpretation of that part which lies immediately in front of the commissura cerebellaris. If this part is a cerebellum, as I have tried to show (1919), then the posterior limit must lie some distance in front of this commissure. If the mesencephalon is the entire part in front of the commissure, as CONEL (1929, 1931) and JANSEN (1930) maintained, the commissure constitutes the posterior limit of the mesencephalon on the dorsal side of the brain. Provisionally



VOL
27
194

I will now consider that portion of the brain which is situated between the frontal border of the commissura posterior and the commissura cerebellaris to be an unit. In the ventricular wall of this brain part there are three sulci (figs 35, 36). The most important of these begins somewhat dorsally to the tuberculum posterius (figs 34, 35, 36 *s.l.*). From this point it extends to below the commissura cerebellaris, crossing to the medulla oblongata. There it is at first rather indistinct, then growing more conspicuous, and finally deepening considerably at the caudal end of the oblongata. This sulcus is the sulcus limitans His. It separates the ventral motor columns from the dorsal sensory columns. In *Bdellostoma* embryos the mesencephalic part of this sulcus is called by CONEL the sulcus isthmi. In *Bdellostoma* embryos of different ages the sulcus isthmi seems to be variable, sometimes beginning dorsally to the tuberculum posterius and ending already in front of the commissura cerebellaris, sometimes beginning above the tuberculum posterius and continuing backwards as the sulcus limitans, sometimes beginning behind the tuberculum posterius at the fovea isthmi and running into the rhombencephalon. In the latter case it is possible to consider it to be a sulcus isthmi (sulcus intraencephalicus posterior of KUPPFER) combined with the sulcus limitans of His. The other mesencephalic sulci lie dorsally to the anterior end of the sulcus limitans and the tuberculum posterius. These sulci are longitudinal grooves belonging to the mesencephalon. The most ventral of them runs through the middle of the mesencephalon and joins the sulcus limitans some distance in front of the cerebellar commissure. The ventral of these sulci is probably the sulcus lateralis mesensephali, separating the tectal part from the subtectal (tegmentum mesencephali?). The most dorsal of the mesencephalic sulci joins the sulcus lateralis frontally, extending caudo-dorsad, and is seen for a short distance in the dorsolateral wall of the mesencephalon. A transversal section through this brainpart thus shows that it contains three sulci separating four cell columns, two dorsally and two ventrally to the sulcus lateralis. These four columns answer to some extent at least to the four columns which PALMGREN has distinguished as generally present in the mesencephalon in vertebrates. It may, however, be pointed out that the tectum mesencephali forms a fifth column, according to PALMGREN. But the limit between the tectum and his dorsal column does not appear, in early embryos at least, to be well pronounced. It seems possible therefore to regard the dorsal column of PALMGREN and the tectal formation as parts of the same unit. A section taken near the posterior pole of the "mesencephalon" has but one column dorsally to the sulcus limitans. A close inspection of this column shows that it causes a considerable swelling on the ventricular wall and the cells are more densely arranged than in the sections preceding it. This nucleus extends caudally to the upper (lateral) border portion of the medulla oblongata, where the extended portion forms the acoustic lobe, dorsally to the sulcus limitans (fig. 37

*cer.?,cer.*). The strong exvertion of the fossa rhomboidalis causes the lateral position of the lobus acusticus. From the dorsal aspect the nucleus in question occupies the caudal part of the "midbrain". A remarkable fact concerning this brain part is that the cerebellar commissure contains a bundle of fibres which turns frontad and splits up in this brain part (fig. 33 *cer.com.*). The other fibres of the commissure can be followed to the frontal end of the lobus acusticus, where CONEL has with some hesitation suggested the presence of a cerebellar portion. It seems to me that there is strong evidence in favour of accepting the presence of a not insignificant cerebellar portion of the "midbrain" in front of the cerebellar commissure. How the future of this cerebellum will turn out the single *Myxine* embryo considered here does not indicate. Meanwhile, as my second embryo indicates, the cerebellar commissure grows stronger and becomes surrounded by nerve cells, showing a distinct progressive development. As already remarked, the figures published by CONEL indicate a certain considerable growth of the commissure. Is it not possible, then, that as the posterior "fontanella" becomes closed, the commissural plate may develop into the cerebellar lobe, there forming the tectal commissures and the "posterior commissure" of JANSEN? In that case it seems very improbable that the posterior commissure could shift so far caudad, as has been presumed by this author. CONEL's material does not seem to have afforded any evidences of such a shifting. We must therefore await new and better material before a decision on this important point can be taken.

*The medulla oblongata, the nerve roots and the cephalic ganglia.*

The external shape of the medulla oblongata is seen from the figures. Here I may point out a few features perhaps worth mentioning. The triangular fossa rhomboidalis is frontally very broad, about twice as broad as long. It is covered by an epithelial membrane which bulges out at the fronto-lateral corners of the medulla, forming quite epithelial auricles (fig. 32 *aur.*). These have nothing to do with the "auricular lobes" in the adult brain, from which the trigeminal roots issue. On a level with the exit of the motor V nerve there is a distinct lateral swelling (of the lateral wall of the medulla). This swelling seems to represent the trigeminal lobe of the adult brain. The width of the fossa is correlated with the great exversion of the dorsal parts of the side wall of the medulla oblongata, which are nearly horizontal. The ventral part of the ventricular wall is vertical, so that the ventral part of the ventricle is reduced to a deep and narrow vertical cleft. The ventricle of the medulla oblongata is thus, at least in its frontal and medium parts, broadly T-shaped in a transversal section. On a level with the anterior part of the auditory capsule and ganglion the horizontal part has decreased to such an extent that the ventricle is reduced to a vertical slit, covered dorsally by a narrow epen-



VOL.
27
194

dymatic membrane and ventrally by the ventral commissural layer of the medulla.

The ventricular wall of the spinal part of the medulla is divided into two about equal parts by the very conspicuous sulcus limitans His, which runs longitudinally. Frontally this boundary sulcus proceeds frontad along the exverted horizontal portion of the medulla. On its way the sulcus bends laterad through the fossa rhomboidalis and comes nearer to the lateral border of the medulla. In the anterior half of the medulla the sulcus becomes less pronounced, partly indistinct, then again becoming sharply defined as it enters the midbrain. The sulcus limitans His generally marks the boundary between the ventral motor and the dorsal sensory columns of the spinal chord, and this also must be the case in the *Myxine* embryo. Ventrally to the sulcus limitans the ganglionic layer of the medulla is divided into a dorsal viscero-motor and a ventral somatic motor column (fig. 37 *v.m.c., s.m.c.*). From the lateral aspect of the ventricular wall the two parts seem to be about equal in extension. The viscero-motor part occupies a considerable part of the exverted wall portion; the somatic motor column is located outside the vertical part of the ventricle. From the lateral aspect of the (lateral) surface of the medulla the viscero-motor column is only visible as a relatively narrow longitudinal band. The somatic column is seen as an even narrower band running ventrally to the visceral. From the ventral exterior aspect the somatic motor columns form a broad band on each side of the ventral commissural bed (fig. 34). Outside this column runs the viscero-motor column as a rather narrow band.

The two sensory columns could not be separated in my embryo. On the ventricular side the united columns form a frontally broad, caudally narrower border-portion of the exverted part of the medulla oblongata. In the spinal portion this part forms a high vertical field. On the outside of the medulla oblongata the columns occupy its entire dorso-lateral surface, owing to a thick cell lamella which from the ventricular part bends laterad as a large tongue (fig. 37 *o.l.t.*) overlapping the dorsal motor column on its outside, so that only a minor part of it is visible on the outside. Parts of the viscero-motor column — with the motor V and VII centres — are probably connected with the lower lateral portion of this tongue.

In the spinal part of the medulla oblongata and in the spinal cord of my embryo the different columns are no longer discernible. This is probably due to insufficient preservation of the embryo, as well as to defective sectioning of this part.

The arrangement of the ganglia and their roots could be studied fairly well in my younger embryo. The trigeminal is well separated from the utricular ganglion (figs 32, 34 *g.V*). It consists of three parts: an anterior forming the profundus ganglion (and nerve), a medium part consisting of the maxillo-mandibular ganglion (and nerves). The third part of the ganglion is a narrow

fingerlike (fig. 32 *f.p.*) dorso-caudally directed prolongation of the mandibular ganglion. This prolongation perhaps may represent the facial ganglion which could not otherwise be demonstrated. The motor trigeminal issues separately behind the mandibular ganglion. The trigeminal ganglion is connected with the brain stem by means of a (not determinable) number of roots (five have been indicated in the fig. 32).

The utricular ganglion (figs 32, 34 *g. VII*) is a rather large ellipsoid body connected with the medulla oblongata by a weak dorsal root. The hyomandibular nerve issues inside this ganglion and becomes visible at its caudal border.

The saccular ganglion (figs 32, 34. *VIII*) is an ovoid body located somewhat obliquely to the axis of the medulla, with its anterior part lying dorsally and the posterior ventro-medially. The root of the ganglion issues rather high up on the medulla. The ganglion seems to be divided into two portions, an anterior with densely crowded and a posterior with more videly dispersed cells. Two acoustic nerves are present (n. utricularis and saccularis).

Inside the posterior part of the auditory capsule the glosso-pharyngeal and vagus roots are located in a longitudinal row (*IX, X*). There is no difference between the glossopharyngeal root and those of the vagus. There are also no ganglia belonging to the two nerves in the neighbourhood of the brain, but the ganglia seem to be located on the nerves a long distance away from the brain.

In a newly hatched *Bdellostoma* NEUMAYER says that there is a glossopharyngeal as well as a vagus ganglion just outside the medulla oblongata. No such a condition could be discovered in *Myxine*.

A ramus recurrens VII, described by NEUMAYER in *Bdellostoma,* is not present in *Myxine*.

*The spinal chord.*

Already in the posterior part of the medulla oblongata the central canal is reduced to a vertical slit, of which the inferior part is somewhat widened in a lateral direction. Through the medium portion of the slit runs the sulcus limitans of *His,* well-defined. In the spinal chord the canal retains its slit-like shape but becomes widened ventrally, medially and dorsally, so that it acquires the aspect of three parallel tubes lying one above the other. Between the "tubes" the epidymal layers of the two walls lie close together and are in many cases joined together. The medium tube represents the sulcus limitans of His. Occasionally the slit is widened so that the three tubes together form a single wide space, in which the sulcus limitans is no longer discernible. Such widened parts are probably artefacts, due to uneven pressure from the fluid contained in the central canal at the moment of preservation.

In the 43-mm specimen the central canal of the spinal chord consists of the



VOL
27
194

two ventral "canals", the uppermost being closed by ependyme. The ventral "canal" is strongly ependymated. The ependyma of the medium canal is very thin. In the adult, the rudiments of the dorsal canal have mostly disappeared. Occasionally, however, there are small vesicles present which represent rudiments of this part of the central canal. The ventral "canal" contains the fibre of REISSNER, which in the 43-mm specimen begins in the strong ependyma (Organon subcommissurale, BERGQUIST) behind the "epiphysis" just in front of the commissura posterior.

## 12. THE VASCULAR SYSTEM.

In my younger *Myxine* embryo the essentials of the vascular system could be studied to some extent. As the system of the bloodvessels has not been investigated hitherto either in *Bdellostoma* or in *Myxine* embryos, one can a priori expect to find some interesting features in the embryo, but it could not be foreseen that the differences with reference to the adult conditions were as considerable as they really are.

### A. THE ARTERIAL SYSTEM.

*The branchial part.*

From a very short unpaired ventral aorta (*Truncus aortae*) (fig. 42 *tr.ao.*) there issue two pairs of arteries, viz. the paired ventral aortae (*p.v.a.*) and a pair of posterior arteries which I have called — anticipatory — the arteries of the ductus intestino-cutaneus (*a.int.cut.*). This artery at first runs caudo-dorsad, then turns fronto-dorsad, ultimately joining the unpaired dorsal aorta (*u.d.a.*) (see below). The paired ventral aortae run frontad and send out the six afferent branchial arteries (*a.b.a.*) to the branchial sacs. The paired ventral aortae, after giving off the most frontally placed of the afferent branchial arteries, join what I shall here call the paired dorsal aorta (*p.d.a.*). The latter runs (one on each side) along the dorsal margin of the branchial region. It receives six pairs of short arteries (*eff.b.a.*) coming from the gill sacs. These represent the efferent branchial arteries. The dorsal paired aorta — in my younger embryo — joins the dorsal limb of the artery of the ductus intestino-cutaneus a small distance in front of its caudal angle. At this point the two intestino-cutaneus arteries are connected by a short commissure (*com.*). The dorsal limb of the artery of the ductus intestino-cutaneus runs into the unpaired aorta about on a level with the mid-portion of the branchial region. Before entering the dorsal aorta the paired artery becomes unpaired for a very short distance (*u.p.*).

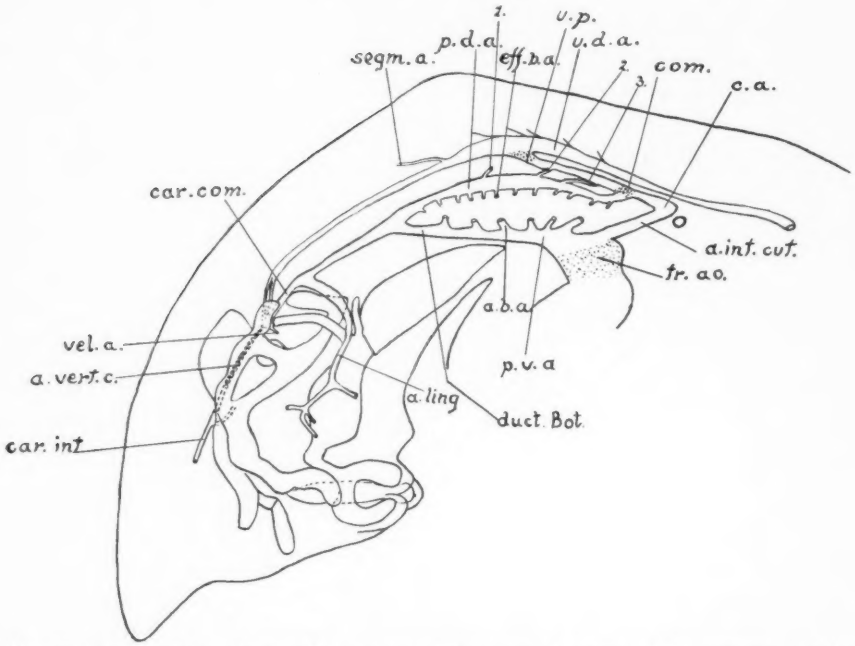


Fig. 42. Reconstruction from serial sections of the arterial system of the younger *Myxine* embryo. 22 ×.

From the branchial part of the paired dorsal aortae issue, on the left side, three dorsal branches (fig. 42 *1.2.3.*). On the right side only two such branches are well developed, but a third is also present, though it is quite insignificant. The branches on the left side are: 1. a small twig issuing on a level with the third pair of efferent branchial arteries. The end of this twig is closed. It is directed toward the point where the dorsal limb of the artery of the intestino-cutaneus duct opens into the unpaired dorsal aorta. 2. a branch issuing from the level of the fourth pair of efferent branchial arteries. It opens into the dorsal limb of the intestino-cutaneus artery. 3. a third branch issuing from the level of the fifth efferent branchial artery. It also opens into the "intestino-cutaneus" artery, behind the preceding one. On the right side the foremost branch is very inconsiderable, indicated only by a strand of mesenchyme and without a lumen. It is found somewhat behind the level of the first branch of the left side. The second branch of the right side issues from the level of the third pair of efferent branchial arteries. It opens into the unpaired part of the dorsal limb of the intestino-cutaneus artery near the place where it joins the dorsal unpaired aorta. The third branch of the right side issues from the level of the fifth pair of efferent arteries, somewhat behind the level of the corresponding branch of the left side.

In the older embryo (fig. 43) the ventral aorta is unpaired from the heart

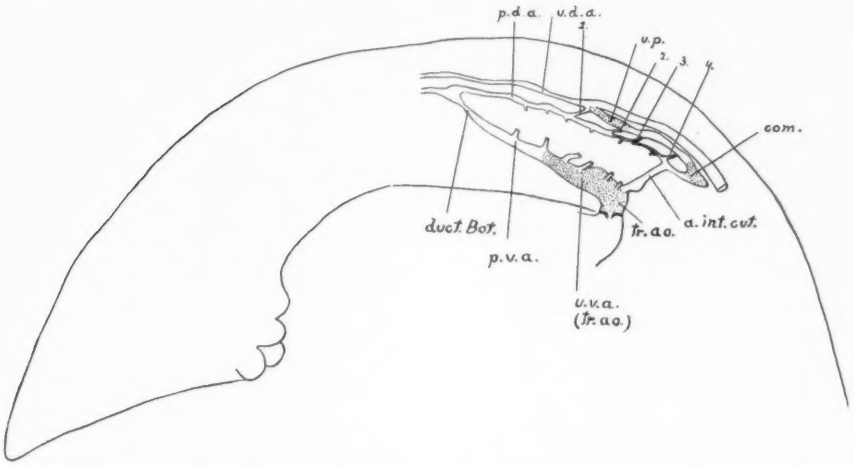


Fig. 43. Reconstruction from serial sections of the arterial system of the older *Myxine* embryo. 17 ×.

to the second afferent artery, then paired. It is obvious that the originally paired ventral aortae have fused from behind frontad. The artery of the intestino-cutaneus duct is also present in this embryo, but differs considerably from that of my younger embryo. Its dorso-frontal end is unpaired for a considerable length and its posterior commissure lies where the lower and upper limbs meet. This commissure is very strong. The paired dorsal aortae join the upper part of the ventral limb of the intestino-cutaneus artery below and frontally to its posterior commissure. The left paired dorsal aorta joins the dorsal limb of the intestino-cutaneus artery through four connecting arteries, of which the two anterior connect up with the anterior unpaired, the two posterior with the paired portion of the intestino-cutaneus artery. These two posterior artery connections are rudimentary, with a lumen only at the end where they issue from the paired dorsal aorta. They have apparently grown out from the latter. These connecting arteries issue on a level with the third, fourth, fifth and sixth efferent branchial arteries respectively. Only two of them are present on the right side viz. the first, which, however, does not open into the intestino-cutaneus artery but ends closed in the mesenchyme near this artery, and the third, which is complete, opening about opposite the third on the left side. The observations on the right side lend further support to the conclusion that these arteries grow out from the paired dorsal aorta.

The two embryos thus differ in regard to the connections of the paired dorsal aortae with the intestino-cutaneus artery, as the aortae in the younger embryo join the dorsal limb of that artery, in the older the ventral one. In the younger there are only three secondary connections, in the older four. These differences are probably due not to the different age of the two stages,

but rather to a certain variability in the behaviour of the lateral aorta in relation to the intestino-cutaneus artery. In the younger embryo the lateral aorta itself forms the connection between the level of the sixth efferent branchial arteries and the dorsal limb of the intestino-cutaneus duct, whereas in the older embryo such a connection is formed secondarily by a branch of the aorta, the aorta proper opening into the ventral limb of the intestino-cutaneus artery. In both cases the result will ultimately be that the lateral aortae on both sides will be connected with the dorsal aorta, as will be explained below.

After joining the ventral aorta the paired dorsal aorta runs frontad to the skull. As it reaches the level of the first internal branchial arch of the pharyngeal basket, it sends off a ventral branch at about right angles (fig. 42 *s.ling.*). This branch soon turns frontad and could be followed to the tooth plate (mandible) and to the basal skeleton. The paired aorta proper soon joins that of the other side (fig. 12 *l.d.aort.*) Then follows a rather long unpaired part (arteria vertebralis capitis) below the basis cranii (*a.v.cap.*). The unpaired dorsal aorta (*d. aort.*) enters this unpaired part frontally. Previously, however, it has sent off a lateral branch on each side (arteria vertebralis lateralis, *a.v.l.*), which joins the anterior portion of the system of the lateral dorsal aorta (arteria carotis communis, fig. 12 *carot.com.*).

The aortic system of the embryo differs very much from that of the adult *Myxine,* in fact so widely that there are many obstacles in the way of a satisfactory interpretation. In the adult there is generally an unpaired ventral aorta sending out six pairs of afferent branchial arteries. The efferent branchial arteries join a longitudinal vessel, connected with the dorsal aorta by means of four pairs of aortic branches, one pair for each pair of the four posterior branchial sacs. The longitudinal vessel on each side continues as the carotid artery frontad and divides into the "inner carotid" of the dorsal part of the head and the "external carotid" of its ventral part. In the Myxinoids some variations have been recorded, for instance by J. MÜLLER. Thus, the ventral aorta is either unpaired throughout or consists of an unpaired posterior half and then of a paired portion or else it is paired throughout (in a *Bdellostoma*-species). The number of efferent branches of the dorsal aorta is also different, 4 in *Myxine,* 5 in *Bdellostoma forsteri.* In the latter, and also in *Myxine,* J. MÜLLER found a rudimentary "ductus Botalli" on each side between the anterior end of the ventral aorta and the "carotis" (paired dorsal aorta). This ductus Botalli corresponds to that part on the ventral aorta which connects with the paired dorsal aorta.

In the adult the following larval vessels are missing: the artery of the intestino-cutaneus duct with its commissure and its connection with the dorsal aorta and the direct connection between the anterior end of the ventral aorta and the "carotis" (paired dorsal aorta). In addition the ventral aorta is mostly unpaired in the adult, paired in the embryos. In the adult the unpaired dorsal

aorta has four connections (for the four posterior branchiae) with the paired, whereas the embryo has none, except that of the artery of the intestino-cutaneus duct.

How have these transformations taken place? A step towards an explanation is suggested by my second *Myxine* embryo (fig. 43. This embryo is somewhat older than that which was used for the preceding description. Fortunately its state of preservation was not too poor to permit a reconstruction of the essentials of the aortic system of the branchial region.

It is obvious that the four arteries which issue from the paired dorsal aortae in the embryo are the same as those which in the adult connect these aortae with the unpaired dorsal aorta. But in the embryo they connect with the intestino-cutaneus artery, which lies close to the unpaired dorsal aorta. The question is now: how have they shifted over to the latter? There is but one way to explain this shifting, viz. through a fusion of the upper limb of the intestino-cutaneus artery with the dorsal aorta. This process has already begun in the embryo as the originally paired intestino-cutaneus artery has become unpaired frontally through the fusion of its two counterparts. The next step will be that this unpaired portion fuses from in front with the dorsal aorta, whereby the four arteries successively shift over to the dorsal aorta. The next step in the transformation would be that the lower portion of the intestino-cutaneus artery became obliterated and disappeared, and that the anterior connection ("ductus Botally") between the ventral aorta and the paired dorsal aortae likewise disappeared (figs 42, 43 *duct.Bot.*).

So far it seems possible to explain the transformations of the aortic system of the embryo into that of the adult, but there remains for us to interpret the peculiar system of the embryo. Owing to the lack of detailed observations on earlier embryonic stages, the explanation given below has only the character of a rather vague hypothesis.

DEAN (1899) has published a few remarks about the development of the heart of *Bdellostoma*. There is not much enlightenment to derive from these. So much, however, is clear, that the earliest development of the heart begins in front of the head through the confluence of vitelline blood vessels to form a medial stem (the heart). Later the heart rudiment is overlapped by the head and drawn in a caudal direction. In an evolutional stage wherein 13—14 gill-slits are present, the heart lies on a level with the third or fourth gill-pouch. In such a stage (DEAN's figures 111 and 122) the ten posterior pairs of gill-slits are located on a gill-lappet expanded on the yolk-mass on each side of the midline. In this stage the heart sends out two posteriorly directed blood-vessels which follow the outer (lower) rim of the lappet. As these vessels follow the external rim of the lappet, which later becomes the ventral, it is obvious that they represent the branchial aortae, from which the afferent branchial arteries start. In a living *Bdellostoma* embryo with 13—14 gill-slits,

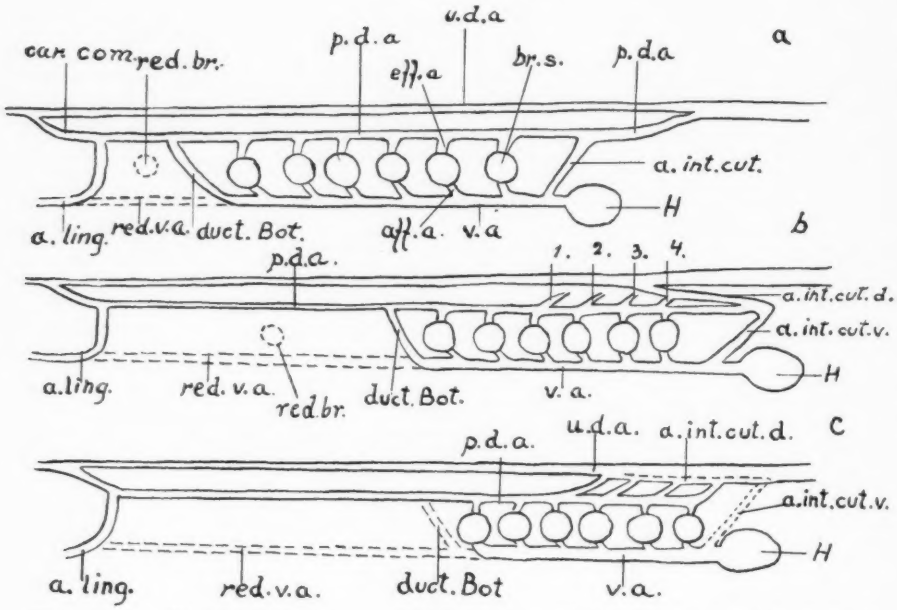


Fig. 44 a—c. Diagrammatical representation of the evolution of the arterial system in *Myxine*.

illustrated by DEAN (fig. 49) he has indicated the presence of branchial arteries with red dots between the slits. But in the very summary descriptions nothing is said about afferent arteries (either in this stage or in any other of the younger stages). Thus the afferent branchial arteries probably issue, in the early embryos, from a caudally directed branchial aorta on each side, whereas in the adult they issue from a frontally directed ventral aorta. The following explanation may be possible. DEAN's figures show that with regard to the branchial slits the heart shifts caudad during development. This process must have taken place by degrees. As it took place when the blood circulation was already established, the continuity of the heart and the arteries could not be broken during the transformation. In the diagrammatical figures 45 a—d I have illustrated how, in my view, this transformation has taken place. It is not neccessary to explain these figures by means of a description. This series would be of very little interest if it were manifestly hypothetical. Fortunately, however, the work of BASHFORD DEAN on the development of *Bdellostoma* furnishes a stage (his figure 124) which corresponds closely to the hypothetical figure 45 c. In this embryo there issues from the upper end of the truncus aortae a group of four afferent branchial arteries in about the same manner as in my hypothetical figure 45 c. I cannot therefore doubt the correctness of my interpretation of the transformation.

Thus far it is possible to arrive at an understanding of the aortic system,

but when it comes to the dorsal part of the system greater difficulties arise, as the early embryos investigated by DEAN have not been described in regard to the aorta dorsalis. The only available embryological data are those of my preceding description of two rather advanced embryonic stages. The essential point of these series is the occurrence of a longitudinal artery (here called the paired dorsal aorta), on each side, into which run the efferent arteries of the gills. Each longitudinal artery had originally but one outlet into the unpaired dorsal aorta (fig. 44 a), into which no efferent branchial arteries run. This outlet, together with the longitudinal artery, form the paired (lateral) dorsal aorta, comparable with that in other fishes. The paired dorsal aortae became secondarily four connections with the unpaired aorta. These connections grow out of the paired vessels (fig. 44 b). As soon as these connections have been established the primary connection disappears (fig. 44 c). Originally the paired dorsal aorta and its outlet into the unpaired probably formed an almost straight vessel running from in front caudad to its opening into the unpaired dorsal aorta (fig. 44 a). As the branchial region shifted caudad, the proximal part (the outlet) of the paired aortae became directed frontad and assumed the position which is characteristic of that in my two embryos (figs 42, 43).

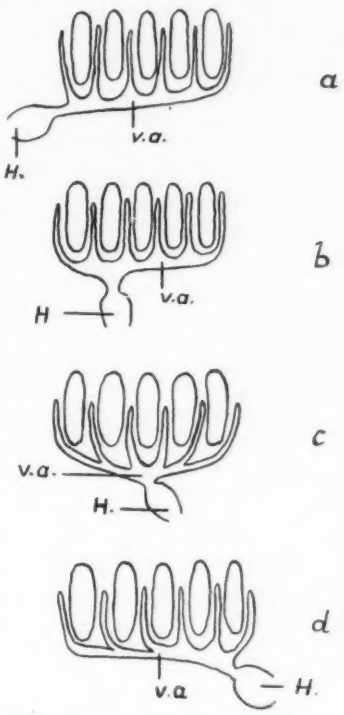


Fig. 45 a—d. Diagrammatical representation of the shifting of the heart and the branchial aorta in *Myxine*.

The preceding interpretation of the aortic system involves the introduction of a partly new conception of the dorsal aorta, as it introduces the idea that a paired and an unpaired aorta were originally present simultaneously. In *Myxine* both aortae are retained, and in most fishes the paired one only, which may, however, fuse from behind on to a secondarily unpaired portion. This theory acquires a certain confirmation from some observations in ray embryos. Thus in 17 to 18 mm embryos of *Torpedo ocellata* there is a short unpaired dorsal aorta jutting out in the mid-line between the two paired aortae. In *Raja clavata* (40—46 mm) and in *Urolophus Halleri* a rudimentary unpaired aorta is also present, but there this rudiment has no lumen. In older embryos of *Torpedo* as well as of *Raja* and *Urolophus* the unpaired aortic rudiment has disappeared.

I have also found a rudimentary unpaired aorta in embryos of *Chlamydo-*

*selachus* (127 mm), *Heptanchus* (77 mm) and *Heterodontus* (54, 62 mm). At least in *Heptanchus* the rudimentary blood vessel becomes embedded in the cartilage of the anterior part of the vertebral column and there distintegrates. The assumption that this rudimentary artery is a primary unpaired aorta is undoubtedly belied by its comparatively late appearance. One would expect that it would already have appeared in such early embryos, in which the lateral aortae had not yet fused caudally so as to become unpaired. This, however, is not the case. On the other hand, if the rudimentary artery were a new formation, it would not disappear almost immediately after its coming into being. In *Scyllium* (*Catulus*) *canicula* an unpaired aorta persists, however, according to CORRINGTON (1930). In *Torpedo* it is present in the 17 and 18 mm stages, but already absent in the 19 mm stage. But in some specimens at least of *Squalus acanthias* this unpaired artery is retained in the basis cranii.

A comparison of the aortic system of *Myxine* with that of a Selachian gives the following points of agreement. In a Selachian the dorsal aortic system consists of the dorsal aorta divided into the two lateral aortae. From the aorta issue the long efferent branchial arteries, one for each gill. These arteries form a loop around each gill compartment. In *Myxine* the efferent arteries are short. There are two for each gill-sac. They form a loop around the internal canal of each gill-sac. The position of this loop corresponds to that of the Selachian. I therefore consider these loops to be homologous. If this conclusion is correct, it is also probably correct to regard the lateral dorsal aortae in both cases as corresponding structures. On the other hand, it may be remembered that in sharks the dorsal aorta is practically unpaired and that this aorta is connected by means of short epibranchials, one for each gill-slit, with a longitudinal vessel from which the loops (efferent branchial arteries) issue (as in *Chlamydoselachus*). The longitudinal vessel has arisen ontogenetically through secondary connections between the epibranchial arteries. This longitudinal vessel might possibly corresponds to the paired dorsal aortae in *Myxine*, although there are strong reasons against such a hypothesis.

1. The "epibranchial" arteries of *Myxine* are secondary connections of the paired dorsal aorta with the unpaired, whereas the epibranchials in sharks are primary connections with the gill-loops.

2. As far as our knowledge goes, the paired dorsal aorta of *Myxine* is formed as a continuous vessel which is united with the unpaired dorsal aorta by means of one primary outlet only (the dorsal part of the intestino-cutaneus artery), which may correspond to the paired aortic root or to a hindmost primary epibranchial artery.

3. In rays, in which the unpaired part of the paired dorsal aortae is particularly short, there is in young embryos a rudimentary unpaired dorsal aorta extending frontad between the two lateral dorsal aortae. A corresponding



VOL
27
194

condition sometimes occurs in sharks. This rudimentary vessel may correspond to the unpaired dorsal aorta in *Myxine*.

4. In early embryos of sharks, as well as of rays, the branchial part of the dorsal aorta is paired throughout. It becomes unpaired later by degrees.

*Phylogenetical considerations.*

The dorsal aorta of *Petromyzon* is unpaired throughout the branchial region. During ontogeny there are no signs in this part of its being unpaired by a fusion of paired vessels. It is unpaired in the youngest embryos as well as in the adult. In front of the branchial region the dorsal aorta becomes paired. But the paired portion already belongs to the head and answers more or less to the carotids, which are always paired. I must thus consider the dorsal aorta to be primarily unpaired in Cyclostom fishes, a conclusion supported by the fact that, according to STENSIÖ (1927), the dorsal aorta of the Silurian Cephalaspids was also unpaired.

VOL. 27 1946

If we thus assume that the aorta dorsalis of *Petromyzon* is primarily unpaired and no paired dorsal aortae are present, we must conclude that the Petromyzonts and Myxinoids belong to widely separated stems of vertebrate development. The ancestral craniote conditions have probably been preserved in *Petromyzon*, whereas the Myxinoids have taken a step in the direction of the Gnathostomians. The latter conclusion is in accord with my interpretation of the mouth parts of *Myxine* as compared with those of a Gnathostomian (HOLMGREN, 1942).

The assumption that the unpaired aorta in *Petromyzon* is primarily unpaired conflicts with the conditions in *Amphioxus* (fig. 46 a). There the branchial part of the dorsal aorta is paired, emitting the branchial arteries and also the dorsal and septal branches. These paired aortae seem to differ from the paired aortae in *Myxine*, as they have dorsal branches for the segmental musculature, branches which are only present on the unpaired aorta in *Petromyzon* (fig. 46 b) and in *Myxine*. It seems reasonable to suppose, therefore, that the unpaired aortae in the latter might have developed through a fusion of the pair of aortae in an *Amphioxus*-like ancestor. The transversal connections may have facilitated such a fusion.

Turning our attention now to *Myxine* (fig. 46 d, e), it is obvious that its paired aorta could not be compared with the paired aorta in *Amphioxus*, as no dorsal intersegmental arteries issue from it but only from the unpaired aorta. The unpaired aorta of *Myxine*, on the other hand, might well correspond to the unpaired of *Petromyzon*. It must be concluded, therefore, that the paired aortae of *Myxine* are a new acquisition on the part of this animal. How this lateral aorta arose cannot be explained with any certainty, but it seems possible that longitudinal connections between the efferent branchial arteries jointly formed it. In such a case an unpaired aorta such as that of *Petromyzon* sent

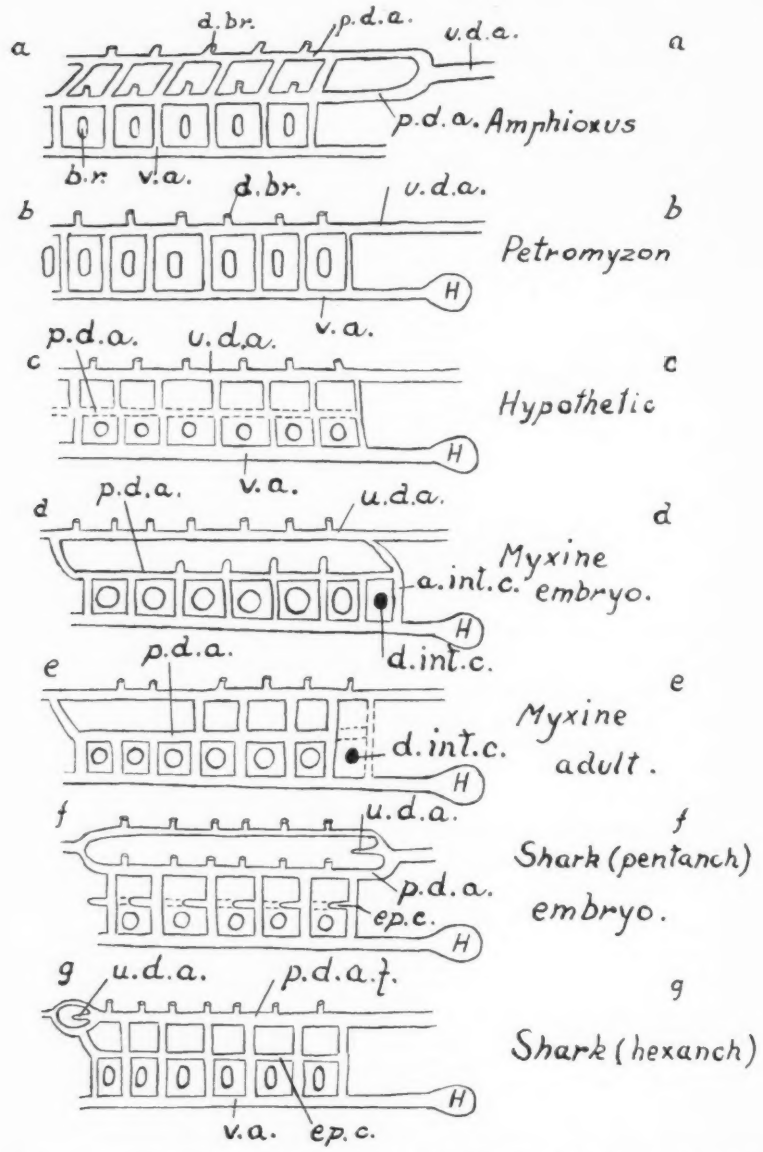


Fig. 46 a—g. Diagrammatical representation of the comparative anatomy of the arterial system in fish.

off primary epibranchials to a longitudinal vessel with which the efferent branchial arteries became connected (fig. 46 c). No such system, however, is present in any living animal. The conditions in the embryonic *Myxine* (fig. 46 d), however, would arise if the primary epibranchials, excepting the

hindmost, were to disappear. Considering that the connections between the dorsal and the lateral aortae in *Myxine* are secondary, it does not seem very probable that the primary connections should disappear, then secondarily reappear. Therefore it seems more likely that the lateral aortae of *Myxine* arose just like the lateral aortae in the Selachians from primary paired rudiments. They then became connected with the dorsal aorta through the four secondary "epibranchials" (fig. 46 a). As, finally, the seventh branchial pocket did not develop any branchial sac but formed the intestino-cutaneus duct, the corresponding branchial artery disappeared.

The next step in the development leads to the conditions in embryonic Selachians, where the *Myxine* conditions return with the important difference that the unpaired aorta dorsalis is rudimentary (fig. 46 f, g) and the paired aortae have taken over its function completely. In the course of development the paired aortae of the Selachians became unpaired (secondarily) in the branchial region (fig. 46 g). The segmental arteries then became connected especially with the unpaired portion of the lateral aortae (CORRINGTON, 1930) and a former condition reappeared, reminiscent of the conditions in *Petromyzon* and partly also in *Amphioxus*. In the adult Selachian the system has been more complicated by the appearance of longitudinal arteries connecting the efferent branchial arteries (epibranchials) dorsally to the branchial clefts (fig. 46 f, g). Such arteries do not develop in *Myxine*, probably owing to the shortness of the efferent arteries. GRODZINSKY (1926) has stated that in *Myxine* the afferent arteries form loops around the lateral part of the branchial sac, whereas the efferent ones form a similar loop around the medial part, these two loops being connected by the capillaries of the gill-sac. According to ALLIS (1911), similar conditions are present in *Chlamydoselachus*, where, however, in both sets of loops the loops are connected with one another at their middle portion. In addition, there are in *Myxine* two efferent arteries for each efferent loop (or branchial sac).

*The "prebranchial" part.*

The ventral aorta of the *Myxine* embryo, after giving off the foremost afferent artery, turns upwards and joins the lateral aorta. This is a condition which, as far as I know, is not met with in any adult fish. In the adult *Myxine*, moreover, this connection is generally missing. This condition in the *Myxine* embryo can scarcely be explained otherwise than by assuming that the connection — the so-called ductus Botalli — represents a branchial vessel belonging to a reduced branchial sac. This explanation is supported by the fact that there is present in this embryo a small rudiment of a gill-pouch (fig. 44 b *red.br.*) on the intestine in front of the formost fully developed gill-sac.

In front of the point where the lateral aorta has received its connection with the ventral aorta, it runs frontad to the head. Upon reaching the level of the branchial skeleton of the head, i.e. of the internal branchial arch, it sends off a strong ventrally directed branch which runs caudo-laterally to this arch, then turning at about right angles frontad, giving off branches especially to the basal musculature (tongue-musculature).[1] This strong artery is generally considered to be the external carotid artery, but its position and general behaviour are hardly reminiscent of those of an external carotid in Gnathostomians. I have therefore sought another explanation better in accord with Gnathostomian conditions.

In early embryos of *Bdellostoma* the branchial region lies partly in the head, partly immediately behind it, with no interruption. As the embryo grew older a cephalic part of the region became separated from a trunk portion. The cephalic gill pockets became reduced, but three or four visceral arches were preserved in a more or less reduced condition. It is obvious that there were originally arterial arches present belonging to this reduced part of the branchial (visceral) system. The least reduced of these anterior visceral arches is the most posterior of them, viz. the first internal branchial arch. Just outside the posterior border of this arch lies the ventrally directed part of the so-called external carotid (figs 42, 44 *a.ling.*). It seems very probable, therefore, that this part of the artery is the branchial artery of that arch, which lost its connection with the ventral aorta as the functional branchial region shifted caudad (fig. 44). If this explanation is correct, the anterior portion of the "external carotid" finds its interpretation as the lingual [(or "afferent mandibular artery" (ALLIS)] artery of certain Gnathostomians.

In the space between the first branchial sac and the exit of the lingual artery the lateral aortae of the adult sends off, arranged more or less in pairs, (5—6) branches — arteriae linguomusculares — (GRODZINSKY, 1926), which run to the strong lingual musculature. These seem to be a serial repetition of the arteriae nutritiae branchiarum described by GRODZINSKY. The latter arteriae issue from the efferent branchial arteries near where they join with the lateral aorta. In the prebranchial portion of the lateral aorta, where efferent arteries are absent, the nutritive vessels open directly in the aorta. If the arteriae linguomusculares and the arteriae nutritiae branchiarum were homologous, the former would indicate that a number (5—6) of branchiae have been reduced in the neck region. In the head two gills must have been present, in the neck portion 5 or 6 and in the branchial region 6. That makes 13 or 14 altogether, which is the sum of the branchial rudiments found by BASHFORD DEAN in the early embryo of *Bdellostoma stouti*. From this point of view the conclusion as to the homology of the two sets of arteries seems to be con-

[1] According to GRODZINSKY in the adult this branch, also has branches to the tentacles and to the nasal canal.

firmed. According to GRODZINSKY, the blood of the arteriae nutritiae flows into the system of the vena jugularis ventralis, whereas that of the arteriae linguo-musculares flows into the left jugular vein. This is a difference regarding the importance of which for the question of homologization I have no opinion.

The interpretation of the "external carotid" as being the lingual artery gains some support by the conditions in *Petromyzon*, where the lingual musculature gets its blood supply by means of the three anterior efferent branchial arteries, which together send blood into the lingual artery. In *Petromyzon* these efferent arteries are at the same time the efferent arteries of the foremost gill-sacs. The difference between *Petromyzon* and *Myxine* would then be that in the latter only the foremost efferent artery ("external carotid" of the authors) sends its blood into the lingual artery and that this efferent artery has lost its respiratory character.

In front of the point of exit of the lingual artery the lateral dorsal aorta turns mediad and joins that of the other side. From this point extends the so-called "arteria vertebralis capitis" (GRODZINSKY). At the posterior end of this artery a strong velar artery is given off on each side. Just in front of where the two aortae meet, each of them receives a thin artery, branched off from the anterior portion of the unpaired dorsal aorta (arteria vertebralis impar of GRODZINSKY). The latter arteria itself joins the posterior end of the vertebralis capitis, where the two lateral aortae join it (fig. 12). In addition, the "vertebralis impar" has some slender connections with its two lateral branches (*a.v.l.*). The arteria vertebralis capitis widens frontally into a large triangular sinus, from the lateral corners of which issues on each side an artery — probably the inner carotid artery — which comes inside the cranial floor and distributes to the brain. This artery could not be studied in detail. A branch of it bends first laterad and then caudad and mediad to the lower side of the brain. This artery is probably the same as that which GRODZINSKY has described in the adult, where it forms a lateral bend, after which it returns to the main artery. This latter could be followed frontad in a position near the ventro-lateral surface of the brain. In the adult *Myxine* it extends into the ethmoidal region, there forming a plexus on the nasal tube (GRODZINSKY).

In the adult there issues from the most anterior portion of the paired parts of the unpaired dorsal aorta, on each side near its entrance into the vertebralis capitis, an artery of which a branch runs to the dorsal surface of the skull, and others to the lateral side of the auditory capsules. This "arteria carotis media" could not be found in my embryos, probably owing to insufficient preservation.

Now arises the question: how are we to interpret these arteries? If the lingual artery cannot be the external carotid, its posterior vertical portion belonging to the efferent branchial system, the anterior portion of the lateral

dorsal aortae must form the carotis system. Then the vertebralis capitis must represent the commissure of the arteria carotis interna that is so characteristic of fishes, and from which the encephalic arteries issue. A carotis externa may then be missing, as it could scarcely be represented by the arteria carotis media of GRODZINSKY, the distribution of which is not the same as that of a carotis externa.

## B. THE VENOUS SYSTEM.

The venous system of the *Myxine* larva is also very unlike that of the adult, in fact so unlike that it is not possible to make a satisfactory comparison. The dissimilarity is really so great that farreaching transformations must take place during the ontogenetical development before the adult conditions can be established.

In my younger specimen the heart is still tube-like, with but slight constrictions between the truncus arteriosus and the ventricle and between the ventricle and the atrium (figs 47, 48). Seen in the frontal projection the tube forms an inverted S-curve (fig. 48) with the atrial end pointing somewhat frontad and ventrad. The venous vessels enter the atrium near its fronto-ventral end (i.e.

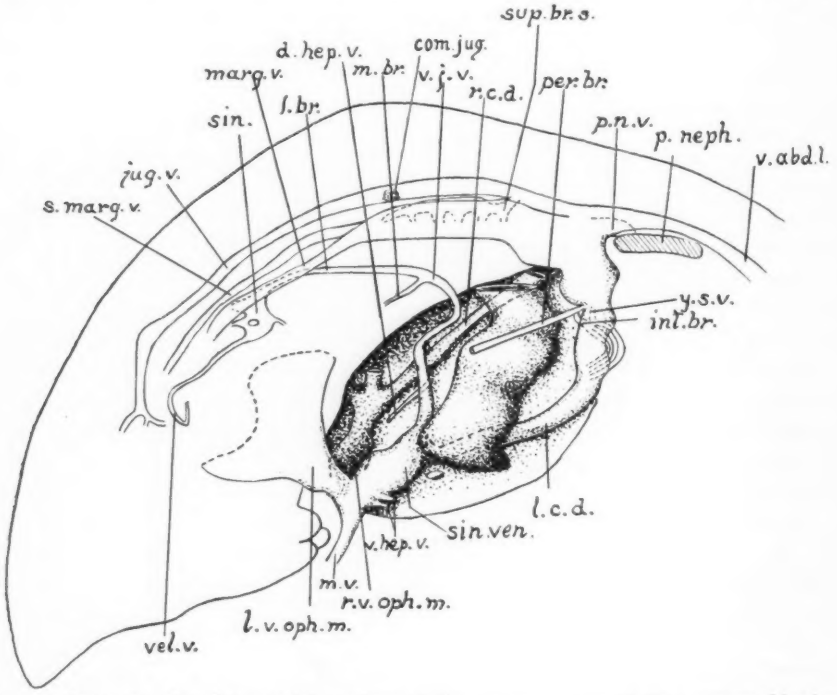


Fig. 47. Reconstruction from serial sections of the venous system of the younger *Myxine* embryo; lateral aspect, left side. 22 ×.

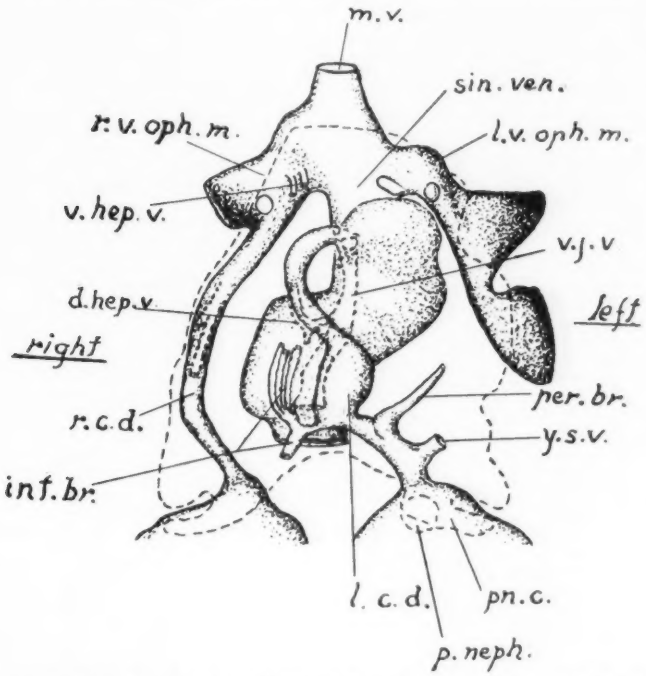


Fig. 48. Reconstruction from serial sections of the principal veins in the *Myxine* embryos, ventral aspect. 31 ×.

near its posterior end). Three veins enter at about the same point, viz. the sinus venosus, the unpaired median inferior jugular vein and the left Cuvierian duct. The heart lies between the inferior jugular vein and the left duct of Cuvier.

The sinus venosus is a very wide vessel (figs 47, 48 *sin.ven.*), which — counting from the heart — runs in a frontal direction. Before it reaches the anteroventral limit of the anterior compartment of the body cavity it broadens considerably and receives a vessel on each side. Both of these vessels are very broad and flat, and cover a wide surface on the yolk sac in the great depression into which the head and neck portion of the embryo is sunk. They apparently represent the omphalomesenteric veins (*r.v.oph.m.*, *l.v.oph.m.*). Numerous smaller yolkveins unite with these broad sinus-like veins. Each of the main vessels, however, joins a longitudinal vein (the posterior cardinal vein of DEAN), running on the surface of the yolk-sac close up along the sides of the embryo and joining in front of the head, there receiving the medial ventral yolk-vein — the so-called liver vein of DEAN. On the right side the main yolk-vein or sinus — already branched before leaving the body cavity — receives the right duct of Cuvier (*r.c.d.*). Frontally the sinus venosus receives a medial vein (figs 47, 48 *m.v.*) running along the bottom of the great wolk

depression. On the right side the sinus receives some small veins (figs 47, 48 *v.hep.v.*) which collect the blood from the ventral liver rudiment.

The medial ventral jugular vein (*v.j.v.*) enters the sinus venosus so near its junction with the atrium that it is not possible to tell whether or not it enters the atrium direct. From the sinus venosus the ventral jugular vein runs nearly straight dorsad to enter the trunk somewhat behind the level of the medium part of the branchial region, a short distance in front of the truncus arteriosus. As the vein passes the dorsal liver lobe (fig. 28 *hep.a.*) it receives a branch (figs 47, 48 *d.hep.v.*) from this lobe. This branch is probably an embryonic vessel which will later disappear altogether. The behaviour of the ventral jugular vein upon entering the trunk will be described below.

The left duct of Cuvier is a rather narrow vessel as it enters the sinus venosus or the heart, but it widens by degrees on its course caudad (fig. 48 *l.c.d.*). At first it follows the liver duct (fig. 28 *hep.d.*) caudad, and as this duct turns dorsad it follows it and enters the trunk at about right angles (fig. 47 *l.c.d.*). In this part of its course it lies on the left side of the widened embryonic intestine. Its further behaviour will be described below. There are two branches of this vein running into the body cavity, viz. one branch collecting from the right side of the proximal portion of the liver duct and from the right side of the widened part of the intestine (figs 47, 48 *int.br.*), where the liver duct runs into it, and another branch (figs 47, 48 *per.br.*) draining the left side of the peritoneal wall. A third branch comes from the yolk sac (figs 47, 48 *y.s.v.*). These branches run into the Cuvierian duct a short distance before it enters the trunk.

The right duct of Cuvier (figs 47, 48 *r.c.d.*) runs along the wall of the body cavity straight to the dorso-caudal corner of its anterior compartment. Its frontal end is connected with the right omphalomesenteric vein. Near this end a peritoneal vein joins it.

We will now consider the median inferior jugular vein (ventral jugular vein) and the Cuvierian ducts after their entrance into the trunk part of the embryo.

The inferior jugular vein narrows somewhat before entering the trunk. Just after it has entered it divides into at least four branches, two lateral (fig. 47 *l.br.*) and two medial (*m.br.*). The lateral branches soon assume a more dorsal position than the two medial and run frontad dorso-laterally to the lingual roll. Somewhat behind the pharyngeal basket the vein suddenly widens to a thin but very high sinus (fig. 47 *sin.*), which receives branches from a dorsal and a medial direction. These branches could not be followed far from their entrance. Frontally the sinus lies externally to the lingual artery and then sends off an anterior vein which runs inside the first external branchial arch, from where it could be followed into the velar fold (fig. 47 *vel.v.*).

The medial branches (fig. 47 *m. br.*) of the inferior jugular vein could be followed some distance frontad, distributing to the lingual roll and further



VOL
27
194

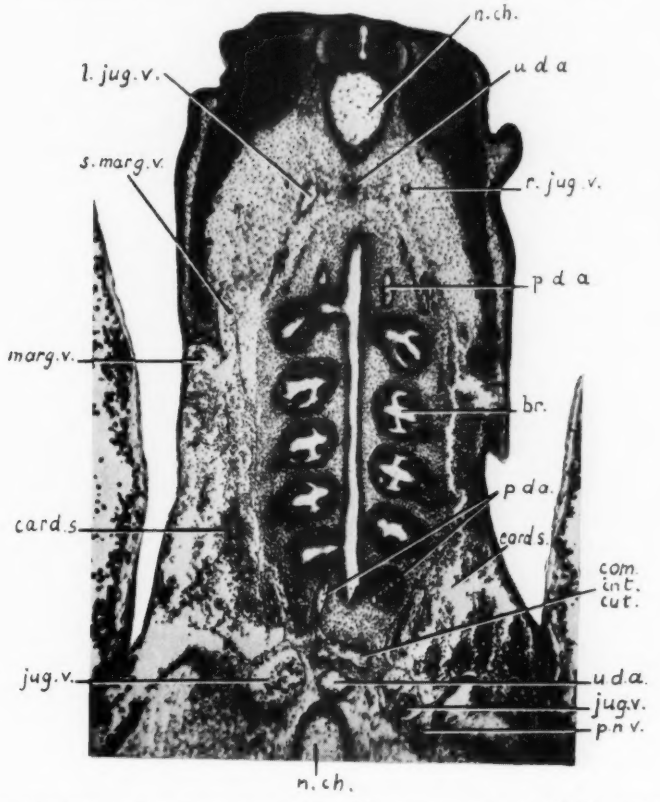


Fig. 49. Longitudinal section through the branchial region of the *Myxine* embryo. 31 ×.

frontad into the ventral part of the head region. Details could not be recognized with any certainty. These medial branches probably correspond to the lingual sinus of the adult as described by COLE (1925).

As the ducts of *Cuvier* attain the trunk they are already very wide vessels. In the trunk they widen still more, forming very wide longitudinal sinuses, which I will call the "cardinal sinuses". In a horizontal section the latter are triangular, in transversal section more irregular. With each cardinal sinus there join up on each side four longitudinal frontally directed veins and two with a caudal direction.

The frontal veins are the anterior cardinal or anterior jugular vein (jugular vein, figs 26, 47 *jug.v.*, 49 *l.jug.v.*, *r.jug.v.*), the marginal (*marg.v.*), the submarginal (*s.marg.v.*) and the superficial branchial sinus. The caudal veins are the short pronephric vein and the long vena abdominalis lateralis.

The anterior cardinal vein enters the cardinal sinus near its caudal extremity (fig. 47 *jug.v.*). It comes from the head region, where three branches could be determined but not followed in detail: one from the lateral head region,

one from below the auditory capsule and one from a point lateral to the velar skeleton. The vein proper lies laterally to the dorsal aorta and has a commissural connection[1] with its vis-à-vis on a level with the second branchial sac. This connection lies close below the dorsal aorta. The nature of the jugular vein of a "vena capitis lateralis" as maintained by NEUMAYER could not be established from my sections.

The marginal and submarginal veins (figs 47, 49 *marg.v., s.marg.v.*) issue from the anterior end of the cardinal sinus. The former runs at the lateral border of the myotomes, somewhat superficially, the latter inside the lateral parts thereof, and thus deeper than the former. These two veins could be followed as far as to the posterior part of the cranial region.

The superficial branchial sinus (fig. 47 *sup.br.s.*) issues from the posterior portion of the anterior cardinal vein. It is a flattened sinus extending frontad to a level with the anterior part of the branchial region. It lies laterally to the branchial arteries but inside the cardinal sinus and the vagus nerve. It receives six branches, one for each gill-sac.

The strong vena abdominalis lateralis (fig. 47 *v.abd.l.*) (parietal vein, lateral cutaneus vein) is connected with the posterior part of the cardinal sinus. It occupies a position in the postbranchial part of the trunk corresponding to that of the marginal vein of the anterior part of the trunk, i.e. at the lateral margin of the myotomes.

Finally, the pronephric vein (figs 47, 49, 50 *p.n.v.*) is a short but rather wide pouch connected with the posterior surface of the cardinal sinus. It lies dorsomedially to the anterior part of the pronephros, but without entering it. In the older embryo small branches of the vein are found entering the kidney, joining a system of veins coming from the yolk sac.

The entire portal and posterior cardinal system could not be studied owing to defective sections.

## C. THE VENOUS SYSTEM OF THE ADULT MYXINE AND OF THE EMBRYO.

In order to obtain a basis of comparison between the veins of the embryo with those of the adult, a summary description of the latter will follow. This description is based on COLE's (1914) reconstruction from serial sections of a 25-cm hag and upon GRODZINSKY's investigation.

In the atrium there opens a very wide but short vein portion called by COLE the sinus venosus. From the frontal end of the sinus venosus issues the unpaired inferior jugular vein. At the posterior and of the sinus venosus follows without any demarcation the "duct of Cuvier". This duct receives frontally

[1] This commissure is not present in my older embryo.

the left anterior cardinal vein, which has a dorsal and a ventral portion, of which the dorsal contains the pronephros of the left side. The two portions join frontally on a level with the atrium. The joined parts are continued frontad in the form of the left anterior cardinal vein proper (superior jugular vein). Caudally the "duct of Cuvier" receives a) two hepatic veins, b) the common posterior cardinal vein with the two posterior cardinal veins proper, of which the left is much stronger than the right.

The veins on the right side are quite different from those of the left. The right anterior cardinal vein has only the dorsal portion with the right pronephros; the ventral is missing. The right anterior cardinal proper is much weaker than the left. It is connected with the left by means of the cardinal anastomosis. This anastomosis is, according to COLE, the only connection between the venous system of the left and the right side. Behind this connection the portal heart runs into the right anterior cardinal. From this heart runs the common portal vein and from it issues the portal or supraintestinal vein.

This peculiar venous system must have developed from that of the embryo, but how this development has taken place cannot be determined, as the differences are too great to allow of a full comparison.

No such full comparison of the embryonic venous system with that of the adult can be made at present. At some few points, however, a comparison is possible. Thus it is obvious that the medial ventral jugular vein of the embryo and of the adult is the same, but here too there are wide differences. In the embryo this vein is unpaired until it penetrates into the trunk; then it becomes paired with two ventral branches from the lingual apparatus and two lateral branches coming from the head region. In the adult the two ventral branches are also present, but there is but one dorsal; this turns over to the right side, where it joins the cardinal heart and the hypophysial and velar sinus and also the anterior part of the right anterior cardinal vein. The left cardinal heart is connected with the left anterior cardinal vein. In the embryo the cardinal heart is not yet developed, but the large sinus (fig. 40 *sin.*) at the posterior border of the skull may represent its rudiment. As to the medial ventral jugular vein, it is thus obvious that this vein was primarily paired and that it became unpaired, the posterior part of the left vein probably being reduced and the anterior part connected with the left anterior cardinal vein. On the right side a middle portion (medium part) of the right anterior cardinal became reduced and the anterior part of it connected with the right median ventral jugular vein.

The Cuvierian ducts of the embryo are scarcely recognizable in the adult and the transformation of the embryonic conditions must be very extensive. The large cardinal sinus seems to have disappeared together with the marginal and submarginal veins, or these may have become transformed into the subcutanean sinuses of the adult(?). There seems to be some possibility of comparing the marginal sinus with that adequately named sinus in the

Cephalaspids, as described by STENSIÖ (1927). This comparison is perhaps supported by the fact that in the embryonic *Myxine* the marginal vein runs ventrally to the lateral border of the cephalic shield. The peribranchial sinus of the adult seems to correspond to the superficial branchial veins in the embryo and the correspondingly named veins in the *Ammocoetes* larva of *Petromyzon*.

Further comparison could not be made as the differences between the adult system and that of the embryo are too great. Perhaps the two broad veins which collect the blood from the marginal vein of the yolk-sac represent omphalomesenteric veins and the marginal yolk veins represent the posterior cardinal veins, as DEAN interprets them? It seems possible that that part of the marginal yolk veins which lies posterior to the "omphalomesenteric" veins may be the cardinals, but those parts which are anterior thereto could scarcely belong to the posterior cardinals since they belong to the morphologically ventral part of the embryo. They may represent the hepatic system of veins (hepatic veins and porta system). In the embryo the rudiments of the liver are drained by special veins, which probably are lost later, to be replaced by the adult system. In the embryo the dorsal liver rudiment, corresponding to the anterior hepatic lobe, has in the adult a special vein which joins the median ventral jugular vein. The ventral rudiment, i.e. the posterior lobe in the adult, is connected with the right side of the sinus venosus where the right omphalomesenteric vein issues from it.

From the preceding discussion it is obvious that a comparison of the embryonic vein system with the adult system in *Myxine* cannot be made without investigating a number of later stages. Such stages are, however, not available.

## 13. THE BODY CAVITY.

The body cavity of my embryos consists of an unpaired wide anterior portion containing the heart with the proximal portions of the big veins running into the heart and the liver and liver ducts, and a paired somotocoelic portion with the pronephros lying (figs 47, 48, 50 *b.c.*) frontally. The pericardial layer covers the wall of the cavity and extends upon the heart, the veins and the liver. The unpaired cavity is found at the bottom of the head depression. Its upper (anterior) surface, which forms the bottom of the depression, is covered by a thin membrane (ectoderm + pericardial membrane). It is depressed medially and rises laterally somewhat up along the wall of the depression. This is especially the case on the left side, where the great yolk veins coming from the sinus venosus leaves the body cavity. The ventral and posterial wall of the body cavity lies directly upon the great ventral yolk-mass. The upper (anterior) surface forms a rather broad field, forming a triangle with an



VOL
27
194

obtuse frontal angle. The side portion of the body cavity extends dorso-caudally as a paired cavity (figs 28, 48 *p.n.c.*), at the ventro-medial wall of which the pronephros is located (figs 28, 48, 50 *p.neph.*). This cavity I will call the pronephros-cavity. It runs immediately into the somatocoel. The outlines of the anterior part of the body cavity are seen in fig. 48. From its lateral aspect the cavity is elliptical in the medial line, as seen in fig. 28, where also the extension of the pronephros-cavity is outlined.

The fronto-ventral right-hand corner of the anterior part of the body cavity is occupied by the liver. The liver complex is surrounded by a mesenchymatic layer inside the peritoneal membrane which covers it. This mesenchymatic layer is frontally thickened, forming, especially in front of the dorsal hepatic lobe, a thick band of cells. This band runs in a dorsal direction and associates with the medial ventral jugular vein, on the right side of which it runs through the body cavity, becoming inserted into the mesenchyma of the trunk where this vein enters the trunk. This band is the rudiment of the septum pericardiaco-peritoneale. Along the body-cavity portion of the left anterior cardinal vein a thin band of mesenchyme runs to the liver capsule, joining that part of it which covers the ventral hepatic lobe, and connects with the posterior part of the alimentary canal. This band represents the early rudiment of the ligamentum hepato-entericum of the adult.

VOL. 27 1946

## 14. THE ALIMENTARY CANAL AND THE LIVER.

In my embryos of *Myxine* the mouth has not yet opened, but the place where it will somewhat later break through is well marked by a transversal, epithelial mouth membrane (figs 16, 28 *st.m.*). As the mouth is then formed, it becomes transversally located, as is pointed out by DEAN. Inside the mouth membrane the mouth cavity, which is located vertically, is very broad, viewed from in front being quadrangular. Its floor (posterior surface) is covered by the rudiment of the broad bulging mandibular complex ("rasping tongue") and in its roof the rudiment of the "palatine" tooth (fig. 28 *pal.t.*) is placed. Then the mouth cavity becomes horizontal and reaches the velar part of the gut. In this part also it is very broad. In this part opens the broad naso-hypophysial duct (fig. 28 *d.n.h.*). In the velar region the gut broadens somewhat still more. The velum consists of two very strong swellings in the dorso-lateral and dorsal wall of the gut (fig. 28 *vel.*). They are so big that they nearly fill the entire lumen of the gut. These swellings meet in the midline so that the gut becomes divided into a dorsal canal and a wide ventral space. The dorsal canal communicates with the ventral space through the narrow slit between the two velar rolls, meeting (in the preserved specimen) in the midline. The canal ends at some distance behind the mid portion of the velum.

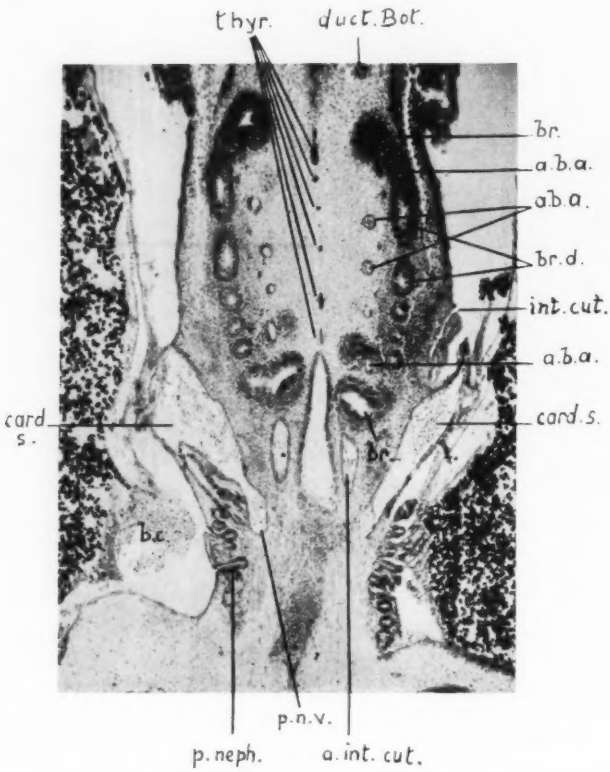


Fig. 50. Longitudinal section through the pronephric region of the *Myxine* embryo. 31 ×.

From about this point the velar rolls unite dorsally in the midline and finally end as a medial unified structure in the roof of the intestine. Behind the velar part the gut constricts rapidly to a narrow tube, which continues caudad into the branchial region. The velar fold ceases on a level with the sixth myotome. Then follows a straight tubelike part of the gut, where the lumen is laterally compressed. This prebranchial portion of the gut lies between the sixth and the thirteenth myotomes. In this space, somewhat nearer the anterior than the posterior end of it, there is in my younger specimen on the left side a rudimentary branchial pocket (fig. 28 *rud.br.*) (on a level with the eighth myotome). Then follows the branchial region with the branchial sacs; these are six on either side. As in the adult, they are placed alternately on the gut. The latter widens caudally from the sixth branchial sac and becomes a very wide sac. In the widened part behind the sixth gill there lies, on the left side, the rudiment of the intestino-cutaneus duct (fig. 28 *d.int.cut.*) and on the right side a rudimentary pouch corresponding to this duct. In the widest part of the alimentary canal opens a wide duct, coming from the body cavity. This

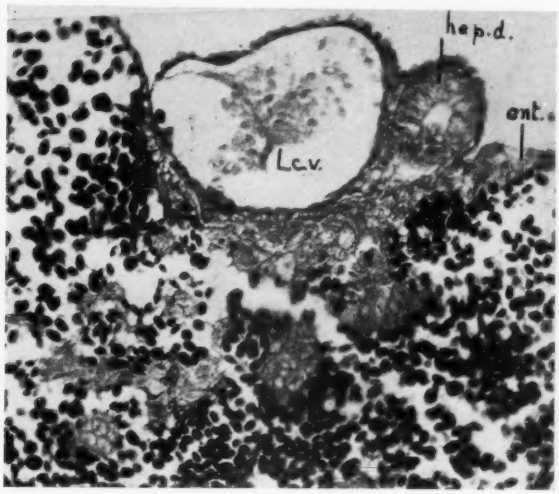


Fig. 51. Transversal section through the ventral wall of the body cavity with the hepatic duct and the left cuvierian duct.

duct is the hepatic duct. Behind the opening of the hepatic duct the alimentary canal (entoderme) continues undifferentiated into the trunk region.

The hepatic duct is very long (fig. 28 *hep.d.*), running obliquely through the body cavity on the right side of the heart. It is accompanied through the body by the left Cuvierian duct. Fronto-ventrally the hepatic duct carries the hepatic rudiments. These consists of a dorsal and a ventral lobe between which the duct is widened into a bladder-like sac. Each hepatic lobe consists of a sac, into which a number of spherical glands open. The dorsal lobe has a short duct opening into the common hepatic duct. The ventral lobe consists of a very wide sac on the ventral surface of which the hepatic acini open. The sac-like part of the ventral lobe represents the rudiment of the hepatic bladder.

The branchial sacs are connected with the gut by means of short ducts. From the sacs lead ducts caudo-ventrally towards the skin. The anterior gill sacs have long, the posterior very short external ducts. They do not yet open on the surface of the embryo, but converge into a great ovoid cell body with which the end portions of the ducts are connected. This body, the construction of which could not be investigated, consists partly of a great mass of epithelial cells and partly of mesenchymatic elements. Its posterior part is pierced by the intestino-cutaneus duct. This duct runs from behind, frontad and ventrad and opens on the exterior outside of the mentioned cell mass. In my older embryo, however, the branchial ducts might be said more or less to open into the same epidermal pocket as the intestino-cutaneus duct, but here too no definite could be obtained, the material not being sufficiently preserved. On

the right side of the embryo, where there is no intestino-cutaneus duct, the body in question is smaller than on the left side.

The inside of the branchial intestine is covered by a high cylindrical epithelium. Where the intestine widens caudally into a wide triangular space the cylindrical cells continue on its dorsal surface as two broad bands separated by a broad groove. Further caudally the bands join medially and the groove disappears. On a level with the pronephros the joined bands again separate and the cylindrical cells are now located beneath the pronephros. The lateral and ventral wall of the widened part of the intestine is covered by the entoderme of the yolk sac. From this entodermal layer broad plasmatic nucleated processes enter the yolkmass dissolving the yolk granules for the nourishment of the embryo (fig. 51).

Immediately ventrally to the branchial part of the gut lies the thyroid gland (figs 28, 50 *thyr.*). It is composed in my younger embryo of a number (about 10) of cell strings, located perpendicularly to the gut. The dorsal portions of these strings are solid, but the ventral are hollow, tubular. The hindmost of these strings reach the point where the ventral aortae issue from the truncus arteriosus. In front of this point the strings end in the mesenchymatic tissue medially between the two ventral aortae. In the older embryo the strings connect ventrally with the unpaired part of the ventral aorta and the truncus arteriosus. Behind this part strings were found between the two arteries of the intestino-cutaneus duct and frontally between the paired parts of the ventral aorta, also somewhat in front of the first gill-sac.

## 15. THE PRONEPHROS.

The excretory organs of the adult *Myxine* have been studied by W. MÜLLER (1875), KIRKALDY (1894), SEMON (1896), SPENGEL (1897) and MAAS (1897). The last-named author investigated some young specimens in which the urinary organs were not yet fully developed. The kidneys of *Bdellostoma* were studied by WELDON (1884), PRICE (1896 a and b, 1897, 1904 and 1910) and CONEL (1917). PRICE's works dealt with the early development of the kidneys of *Bdellostoma stouti*. PRICE's papers of 1896, 1897 and 1904 contain the only investigations ever made into the early embryological development of the kidney in any Myxinoid fish.

According to PRICE (1904) the rudiments of the kidney of *Bdellostoma* in very early stages of development are segmentally disposed, the nephrotome of each segment forming a section of the organ. Each such section consists of the rudiments of a segmental tubule and a small portion of the so-called segmental duct. The duct segments join together forming the segmental duct which apparently corresponds to the pronephric or Wolfferian duct in other

animals. The originally strictly segmental arrangement of the tubules is disturbed as the frontal tubules subsequently are crowded backwards, forming the pronephros. It is also disturbed by the formation of new tubules by the branching of those previously present. At a certain stage of development there are in *Bdellostoma*, on the right side, twenty-one tubules, of which the first three have no connection with the segmental duct, while the last three are connected with Malpighian corpuscles. On the left side the pronephros has nineteen tubules, of which the two first have no connection with the central duct and the two last are connected with the Malpighian bodies and therefore represent closed tubules. At this stage the pronephros is still connected with the mesonephric duct. This connection later becomes severed. The central duct of the pronephros of this stage has only partially a lumen. PRICE says that the cavity at the side of the glomerulus, the cavity of the Malpighian corpuscle, is almost in communication with the coelom. This is interesting as suggesting that in some cases the communication might actually occur, in which case the glomerulus would be virtually in the body-cavity."

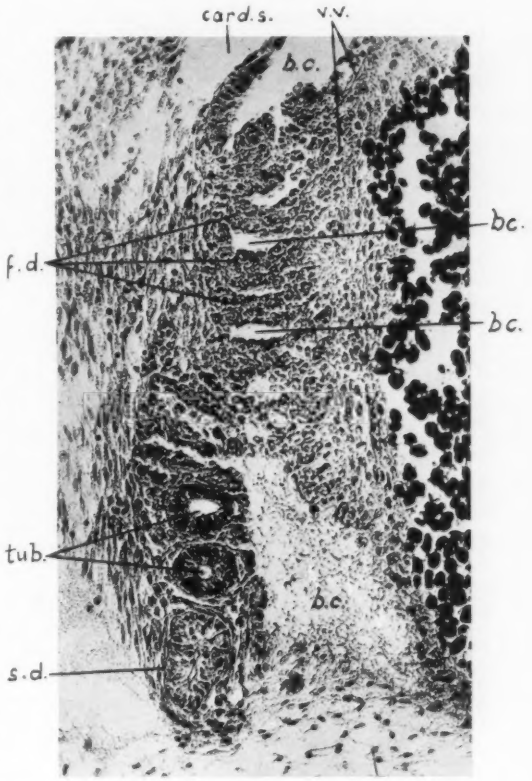


Fig. 52. Longitudinal section through the ventral part of the pronephros with the folds of the wall of the body cavity.

In the embryo here used for the purpose of description — my younger embryo — there are on each side fourteen tubules of the pronephros, which open into the body-cavity with their proximal ends. The distal ends are connected with the somewhat convoluted segmental duct (figs 52, 53, 55, 56 *s.d.*), the lumen of which is for the most part very narrow or altogether missing. The segmental duct continues immediately into the mesonephric duct. The pronephric tubules (*tub.*) are already crowded together and the entire pronephros occupies a space corresponding approximately to the 24th—26th myotomes. By way of comparison it may be stated that the pronephros of a 140-mm *Myxine* is situated opposite the 31st segment. When drawing this

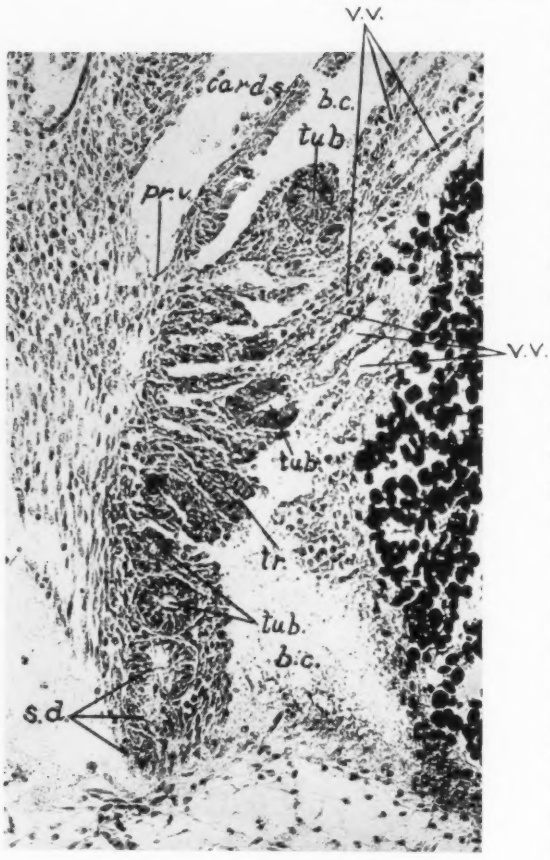


Fig. 53. Longitudinal section through a more dorsal part of the pronephros than that in fig. 52.

comparison it must be borne in mind that there is an increase in the myotomes in front, there being formed at least three segments. If therefore the pronephros has shifted towards the rear, this shifting movement must have been very insignificant. In the adult *Myxine* the pronephros is enclosed in the pronephric vein, which is not the case in the actual embryo. This peculiar position comes about later and is already initiated in the older of my embryos.

In my younger embryos the pronephros lies in the medial wall of the body cavity, dorsally to the wide parts of the intestine. The dorsal wall of the intestine extends laterally to the pronephros. In the pronephric part of the body cavity its endothelial covering is transformed into a rather thick layer of cylindrical cells of secretory appearance disposed in groups with a somewhat lower epithelium between the groups, so that a section through this layer has an undulated appearance. In the vicinity of the pronephros proper, groups of cells are found which consist of a very thin basal portion carrying in its midst a sometimes pedunculated cell body containing the cell nucleus and protruding into the body cavity. Generally the cell body is not pedunculated, though it nevertheless protrudes into the body cavity. This kind of tissue covers those parts of the pronephros which pertain to the wall of the body cavity. As will be suggested below, these peculiar cells of the wall of the body cavity are excretory cells, producing some matter which collects in the body cavity. In a *Myxine* with a body 43 mm long the pedunculated cells (fig. 54) are also present, but there the dorsal wall of the body cavity of the embryo has become lateral. In adult specimens pedunculated cells were occasionally found in the wall of the body cavity.



VOL
27
194

Fig. 54. Transversal section through the lateral part of the body cavity of the pronephric region, with pedunculated cells.

VOL. 27 1946

The ventral wall of the body cavity just below the pronephros is provided with a series of narrow, parallel transversely located folds (fig. 52 *f.d.*), separated by deep and narrow grooves. Medially these folds bend dorsad, entering the medial wall of the body cavity, and they become broader, each now containing the funnel-like opening of a pronephric tubule. In the actual embryo there are 12 to 14 such folds, but I cannot say for certain that there is also one tubule for each fold, as it is possible that a fold might have more than one tubule. The epithelial cells lining the folds are similar to those in the environs of the pronephros already described, with their cell bodies more or less protruding into the body cavity. The same sort of cells are found in the folds and are especially well developed at the basis of the latter.

In three of the posterior folds a bottom portion widens out into a rounded chamber or vesicle (fig. 56 *gl.*), in the bottom of which a cluster of clubshaped epithelial cells of the same nature as those of the rest of the folds is inserted. This cluster fills up a great part of the chamber. They form a glomerulus in which, however, no blood vessels have as yet entered. These glomeruli are not shut off from the body cavity but are in free communication with it. They are thus external glomeruli or glomi. In my 43-mm specimen the communication is considerably widened and two of the glomi lie completely in the body cavity. The communication is also preserved in the adult *Myxine*. In the 43-mm specimen blood vessels have entered the glomi. A characteristic feature of these glomi is the abundance of pedunculated epithelial cells covering its free surfaces.[1] Such cells are also present in the lateral wall of the body cavity in the pronephric region (fig. 54). This wall corresponds to the dorsal wall of the body cavity in the embryo. In the glomeruli the pedunculated cells are

[1] Such cells are also characteristic of the glomi of the adult.

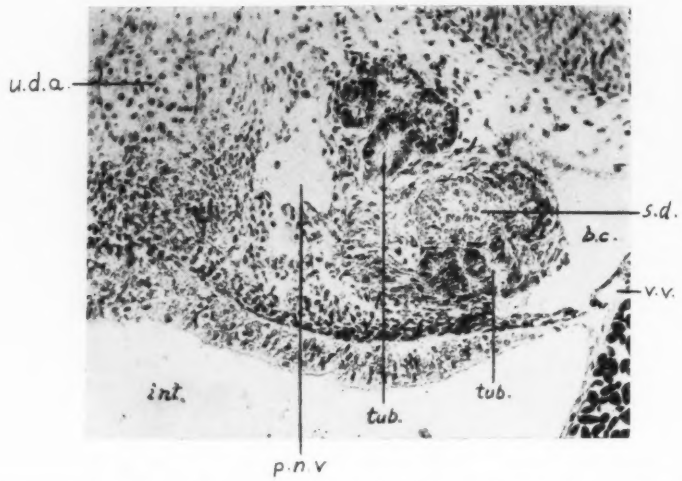


Fig. 55. Transversal section of the pronephros of the older *Myxine* embryo (medium region).

obviously excretory cells; it seems certain, therefore, that the identically formed cells of the body cavity are also excretory cells. The excretory products thus pass into the body cavity.

In the embryo the body cavity has an outlet through the pronephric tubules and the segmental duct. In the adult, moreovver, the abdominal pore forms another outlet. Whether there is also an abdominal pore in the embryo I cannot tell.

The tubules (fig. 53 *tub.*) of the embryo are all short, straight tubes, located perpendicularly to the wall of the body cavity. Their wall consists of a high cylindrical epithelium, consisting of narrow cells with dense, deep staining protoplasm (Azan-Mallory staining). I could not find any trace of cilia on the surface of the cells, but it must be borne in mind that my embryos were but poorly preserved, so that any cilia that might have been present could not be expected to be retained. The tubules open into the somewhat convoluted segmental duct.[1] The epithelial cells forming this duct differ from those of the tubules in their greater size and less easily tingible protoplasm, so that the sections through the duct appear much less coloured than those through the tubules.

The blood supply of the pronephros is not yet fully established in my younger embryo. The pronephric vein does not as yet send any branches into the pronephros but lies close to its anterior part, medially to it. On the lateral side the pronephros is entered by a series of veins (fig. 53 *v.v.*), running immediately beneath the ventral peritoneal epithelium. They enter the pre-

[1] In my older embryo the lumen of the segmental duct is mostly obliterated, and the duct forms a string of more or less irregularly arranged cells (figs 55, 56 *s.d.*).

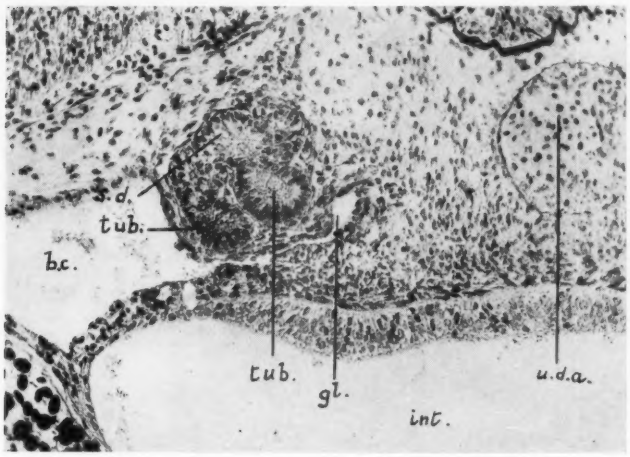


Fig. 56. Transversal section of the pronephros of the older *Myxine* embryo (posterior region).

viously mentioned folds of the wall of the body cavity immediately below their epithelium. As these veins reach the tubules af the pronephros, they seem to form a venous sinus around each tubule. Branches also seem to reach the segmental duct, but no vessels could be discovered leaving the pronephros. In my older embryo the conditions are altered, the pronephric vein having numerous branches which enter the pronephros and are connected with the venous system, entering the kidney from the lateral side. Thus a venous blood-stream passes from the lateral side through the kidney to flow into the pronephric vein. The lateral veins come from the very extensive vein plexus covering the yolk sac of the embryo and connecting up with the marginal vein of the yolk mass (posterior cardinal vein?). Details could not be determined. No arteries were found in connection with the kidney in either of the two embryos.

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## EXPLANATION OF LETTERINGS.

*a.b.a.*, afferent branchial artery.
*a.car.com.*, arteria carotis communis.
*aff.a.*, afferent branchial artery.
*a.int.c.*, arteria intestino-cutaneus.
*a.int.cut.*, arteria intestino-cutaneus.
*a.int.cut.d.*, dorsal limb of the a. intestino-cutaneus.
*a.int.cut.v.*, ventral limb of the a. intestino-cutaneus.
*a.ling.*, arteria lingualis.
*a.o.d.*, dorsal unpaired aorta.
*a.o.d.l.*, arteria vertebralis lateralis.
*aud.*, auditory capsule.
*aur.*, auricle.
*a.v.cap.*, arteria vertebralis capitis.
*a.vert.c.*, arteria vertebralis capitis.
*a.v.l.*, arteria vertebralis lateralis.
*a.v.n.b.*, anterior vertical nasal bar (anterior border cartilage).
*bas.1,2,3*, anterior, medium, posterior basal skeleton pieces.
*bas.1.l.*, lateral basal cartilage 1.
*bas.1m.*, medial basal cartilage 1.
*bas.c.*, basal cartilage.
*bas.c.1l.*, lateral basal cartilage 1.
*bas.c.1m.*, medial basal cartilage 1.
*bas.c.2,3*, second, third basal cartilage.
*b.c.*, body cavity.
*b.c.s.*, border of the cephalic shield.
*b.o.*, bulbus olfactorius.
*b.ot.l.*, basiotic lamina.
*br.*, branchial sac.
*br.1*, first *internal* branchial arch.
*br.2?*, second internal branchial arch?.
*br.d.*, branchial duct.
*br.mes.*, branchial mesenchyme.
*bv.*, blood vessel.
*c.a.*, caudal angle of the arteria intestino-cutaneus.
*car.com.*, a. carotis communis.
*card.sin.*, cardinal sinus.
*car.int.*, a. carotis interna.
*carot.com.*, a. carotis communis.
*carot.int.*, a. carotis interna.
*c.br.*, musculus constrictor branchialis.
*cer.?*, cerebellum?
*cer.com.*, cerebellar commissure.
*c.hab.*, commissura habenularis.
*co.*, corium.
*com.*, commissure of the arteria intestino-cutaneus.
*com.c.*, commissura cerebellaris.
*com.int.cut.*, commissure of the a. intestino-cutaneus.
*com.jug.*, commissure between the jugular veins.
*con.1,2,3*, connections of the dorsal longitudinal bar.
*con.ex.br.1*, connection of the first extra-branchial arch.
*con.ex.hy.*, connection of the extrahyal arch.
*con.ex.pq.*, connection of the extrapalato-quadrate.
*const.br.*, m. constrictor branchialis.
*c.p.*, commissura posterior.
*corn.c.*, cornual cartilage.
*cort.t.*, cortex telencephali.
*c.s.c.*, semicircular canal.
*d.aort.*, dorsal aorta.
*d.br.*, dorsal branch.
*d.end.*, ductus endolymphaticus.
*d.hep.v.*, dorsal hepatic vein.
*d.int.c.*, ductus intestino-cutaneus.
*d.int.cut.*, ductus intestino-cutaneus.
*d.l.b.*, dorsal longitudinal bar.
*d.n.h.*, ductus naso-hypophysialis.
*d.pl.*, dental plate.
*duct.Bot.*, "ductus Botalli".
*e.br.1*, extrabranchiale 1.
*e.br.2*, extrabranchiale 2.
*eff.a.*, efferent branchial artery.
*eff.b.a.*, efferent branchial artery.
*ent.*, entoderme.
*ep.c.*, epibranchial commissure.
*ex.br.1*, extrabranchiale 1.
*ex.br.2*, extrabranchiale 2.
*ex.hy.*, extrahyal.
*ex.pq.*, extrapalato-quadrate.
*ex.pq.+hy.*, extrapalato-quadrate + extra-hyal.
*f.carot.*, foramen caroticum.
*f.d.*, folds of the wall of the body cavity.
*font.1,2*, anterior, posterior fontanella.
*f.p.*, fingerlike process of the V ganglion.
*f.r.*, fasciculus retroflexus.
*g.V.*, ganglion V.

*g.VII.*, ganglion utriculare.
*g.VIII.*, ganglion sacculare.
*ggl.V.*, ganglion V.
*ggl.V.1*, profundus ganglion.
*ggl.V.r.*, root of the ganglion V.
*ggl.VII.*, ganglion utriculare.
*g.hab.*, ganglion habenulae.
*gl.*, glomerular cavity.
*gl.muc.*, mucous gland.
*g.sp.1*, first spinal ganglion.
*H.*, heart.
*hep.a.*, anterior hepatic lobe.
*hep.bl.*, hepatic bladder.
*hep.d.*, hepatic duct.
*hep.p.*, posterior hepatic lobe.
*hy.*, hyoid arch.
*hyp.*, hypophysis.
*hyp.c.*, hypophysial cartilage.
*hyp.com.*, hypophysial commissure.
*hy.th.*, hypothalamus.
*inf.*, infundibulum.
*int.*, intestine.
*int.br.*, intestinal branch (vein).
*int.cut.*, ductus intestino-cutaneus.
*int.+mes.*, pars intercalaris+mesencephalon.
*jug.v.*, jugular vein.
*lab.c.*, labial cartilage.
*l.br.*, lateral branch of the ventral jugular vein.
*l.d.aort.*, lateral dorsal aorta.
*l.jug.v.*, left jugular vein.
*l.s.m.c.*, lateral border of the somatic motor column.
*l.t.*, lamina terminalis.
*l.v.*, lateral ventricle of the forebrain.
*l.v.m.c.*, dorsal border of the visceral motor column.
*l.v.oph.m.*, left omphalo-mesenteric vein.
*marg.v.*, marginal vein.
*m.b.e.*, musculus buccalis superficialis.
*m.b.p.*, musculus buccalis profundus.
*m.br.*, medial branch of the ventral jugular vein.
*m.cl.*, musculus clavatus.
*m.constr.*, musculus constrictor pharyngis.
*m.c.v.e.*, musculus cranii-velaris externus.
*m.c.v.i.*, musculus cranii-velaris internus.
*md.*, mandible.
*md.a.V.*, nervus mandibularis arterior V.
*md.p.V.*, nervus mandibularis posterior V.
*mes.*, mesencephalon.
*ml.1,2,3*, first, second, third mesenchymatic layer of skin.
*m.perp.*, musculus perpendicularis.
*m.sp.v.*, musculus spino-velaris.
*m.tub.*, musculus tubularis.
*muc.gl.*, mucous gland.
*m.v.*, medial yolk vein.
*nas.*, nasal sac.
*nas.d.*, nasal duct.
*nch.*, *n.ch.*, *n.c.h.*, notochord.
*n.ch.d.*, degenerated part of the notochord.
*n.ch.h.*, notochord hook.
*n.com.p.*, nucleus of the commissura posterior.
*n.d.hyp.*, nucleus dorsalis hypothalami.
*n.hy.VII.*, nervus hyomandibularis VII.
*n.md.a.*, nervus mandibularis anterior.
*n.md.p.*, nervus mandibularis posterior.
*n.mx.V.*, nervus maxillaris V.
*n.olf.a.*, nucleus olfactorius anterior.
*n.por.?*, recessus neuroporicus?
*n.prof.*, nervus profundus.
*n.pr.opt.*, nucleus preopticus.
*n.v.hyp.*, nucleus ventralis hypothalami.
*oc.*, eye.
*pal.b.*, palatine bar.
*pal.t.*, palatine tooth.
*p.b.*, polar body.
*p.caud.th.*, pars caudalis thalami.
*p.c.b.*, musculus protractor cartilaginis basalis.
*p.ch.pch. p.c.h.*, parachordale.
*p.d.a.*, paired dorsal aorta.
*p.d.a.f.*, fused paired aortae.
*p.d.th.*, pars dorsalis thalami (pars caudalis thalami).
*per.br.*, peritoneal branch of the left cuvierian duct.
*p.fr.th.*, pars frontalis thalami.
*p.m.th.*, pars medialis thalami.
*pn.c.*, pronephric body cavity.
*p.neph.*, pronephros.
*p.n.v.*, pronephric vein.
*pq.bl.*, palato-quadrate blastema.
*pr.c.*, pronephric body cavity.
*pr.dent.*, musculus protractor dentium.
*pr.v.*, pronephric vein.
*p.v.a.*, paired ventral aorta.
*p.v.n.b.*, posterior vertical nasal bar (posterior border cartilage).
*r.c.d.*, right cuvierian duct.

*red.br.*, reduced branchial sac.
*red.v.a.*, reduced ventral aorta.
*r.jug.v.*, right jugular vein.
*rud.br.*, rudimentary branchial sac.
*r.v.oph.m.*, right omphalo-mesenteric vein.
*s.c.*, sensory column.
*s.ch.*, sperm chamber.
*s.d.* in figs 46—49, segmental duct.
*s.d.*, sulcus dorsalis.
*s.di.tel.*, sulcus di-telencephalicus.
*segm.a.*, segmental artery.
*sens.n.*, sensory nerve.
*sin.*, sinus venosus.
*sin.ven.*, sinus venosus.
*s.l.*, sulcus limitans His.
*s.lim.*, sulcus limitans His.
*s.m.*, sulcus medius.
*s.marg.v.*, submarginal vein.
*s.m.c.*, somatic motor column.
*s.n.c.*, subnasal cartilage.
*sp.1*, first spinal ganglion.
*s.p.g.1*, first spinal ganglion.
*st.m.*, stomodeal membrane.
*sup.br.s.*, superficial branchial sinus.
*s.v.*, sulcus ventralis.
*t.1—4*, tentacular cartilage 1—4.
*t.cl.*, tendon of the clavatus muscle.
*tel.*, telencephalon.
*tent.*, tentacular blastema.
*thyr.*, thyreoidea.
*t.pl.*, tooth plate.
*tr.*, funnel of a tubulus.
*trab.*, trabecle.
*trab.com.*, trabecular commissure.
*tr.a.o.*, truncus aortae.
*tr.olf.hab.*, tractus olfacto-habenularis.
*tub.*, tubulus of the pronephros.
*tub.p.*, tuberculum posterius.
*t.vag.*, tendon of the vagina of the clavatus tendon.
*u.d.a.*, unpaired dorsal aorta.
*u.p.*, unpaired part of the arteria intestino-cutaneus.
*u.v.a.*, unpaired ventral aorta.
*v.a.*, ventral aorta.
*v.abd.l.*, vena abdominalis lateralis.
*v.br.b.*, ventral branchial bar.
*vel.*, velum.
*vel.a.*, velar artery.
*vel.c.*, velar cartilage.
*vel.v.*, velar vein.
*v.hep.v.*, ventral hepatic veins.
*v.jug.*, jugular vein.
*v.j.v.*, ventral jugular vein.
*v.m.*, marginal vein.
*v.marg.*, marginal vein.
*v.m.c.*, visceral motor column.
*v.sm.*, submarginal vein.
*v.submarg.*, submarginal vein.
*v.tr.?*, velum transversum?
*v.v.*, venous vessels.
*v.vel.*, velar vein.
*y.s.v.*, yolk-sac vein.
*1,2,3,4*, secondary efferent branchial arteries.
*I.*, nervus olfactorius.
*II.*, nervus opticus.
*V.*, nervus trigeminus.
*V.1.*, nervus trigeminus I.
*V.2.*, nervus trigeminus II.
*V.m.*, motor trigeminus nerve.
*VII.*, utricularis ganglion.
*VII.m.*, motor facialis nerve.
*VII.s.*, utricularis root.
*VIII.*, saccularis nerve or ganglion.
*IX.*, nervus glossopharyngeus.
*X.*, nervus vagus.

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VOL
27
194

# ON SOME ARCHAIC FEATURES IN THE DEVELOPING CENTRAL STEM OF THE MAMMALIAN CHONDROCRANIUM.

BY

*PER ERIC LINDAHL*

VOL.
27
946

The mammalian skull shows a number of characters relating it to that of primitive Sauropsida. Moreover, other characters seem to have been preserved from still more primitive ancestors. It is to be expected that such ancient features may be found especially in the developing mammalian chondrocranium. As to the central stem, however, the development of its praechordal portion has become modified to such a degree, that in many forms paired structures corresponding to the trabecles are totally missing. It therefore seems to be of special interest to trace primitive features of organisation just in the central stem.

In a pig embryo of 21 mm. body length I have found in the nasal septum a mode of chondrification which seems to reflect earlier phylogenetic stages. The high and thin nasal septum consists to a great extent of a mesenchymal condensation continuing into the interorbital region. The limit between the praecerebral and the subcerebral portions of the septum is determined by the caudal extension of the tectum nasi, marked in fig. 1 by an arrow (*a*). Here the caudal end of the nasal septum, fixed by the caudal extension of the rudiment of the cupula posterior is also marked by another arrow (*b*). The rostral end of the blastema, as well as its dorsal edge in the anterior part of the subcerebral portion of the nasal capsule, are rather diffuse. The chondrification has proceeded so far that a continuous mass of young cartilage extends through the subcerebral and the posterior half of the praecerebral

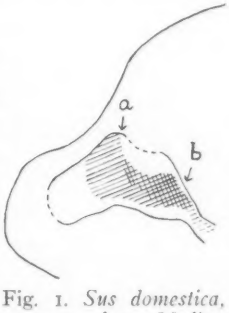


Fig. 1. *Sus domestica*, 21 mm. embryo. Median section of nasal septum and anterior portion of trabecular plate. *a* posterior border of tectum nasi, *b* posterior end of capula nasi. Blastema unshaded, cartilage shaded, blastema and procartilage between the paired cartilaginous septal plates cross-shaded. Reconstruction. 10 ×.

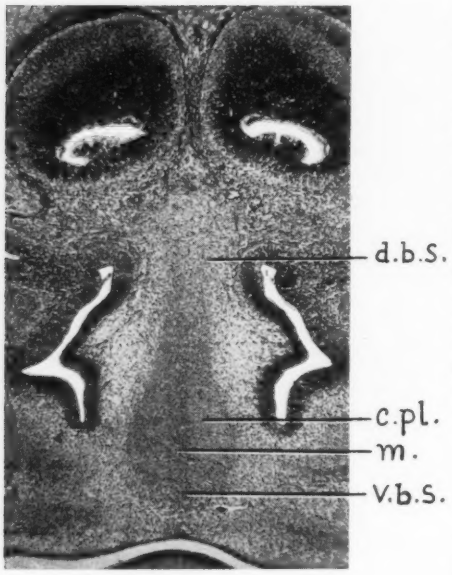


Fig. 2. *Sus domestica*, 21 mm. embryo. Cross section through subcerebral portion of nasal capsule. *c.pl.* cartilaginous plate, *d.b.s.* dorsal paired blastema of nasal septum, *m.* median lamella of procartilage and condensed mesenchyme, *v.b.s.* ventral blastema of nasal septum. 40 ×.

portion of the nasal septum. In pars subcerebralis this cartilage is to a large extent paired, forming two plates of varying height separated by a thin median lamella of procartilage and condensed mesenchyme (fig. 2). To some extent also the blastema dorsal to the two cartilaginous plates shows a paired structure, the two components even bending laterad (fig. 2). The two cartilaginous plates extend behind the cupulae posteriores where they correspond to the anterior part of the trabecular plate (septum interorbitale). They are here less high and are separated caudally from the posterior rod-like end of the trabecular plate by a mass of condensed mesenchyme. In the anterior part of the subcerebral portion of the septum the two cartilaginous plates merge ventrad and rostrad into an unpaired cartilage, which takes almost the whole height of the praecerebral portion of the septum and sends caudad a crescent-like extension ventrally to the paired plates. This unpaired cartilage forms the dorsal edge of the septum joining the chondrified parts of the tectum nasi.

That a similar mode of chondrification occurs in the cat is obvious from TERRY's (1917) description of 12 mm. embryos. "In van Wijhe preparations the ventral part of the septum was stained blue, appearing in the form of two streaks extending from the trabecular plate forward, side by side and separated by a less deeply stained tract."

GAUPP has repeatedly forwarded the opinion that the mammalian nasal capsule compaired with that of reptiles has become caudad extended pushing itself along the interorbital septum under the anterior portion of the cavum cranii. This means that the interorbital septum of the reptiles has become converted into the nasal septum of the mammals and accounts for the common primary loss of a septum interorbitale in mammals (cf. STADTMÜLLER 1936). WEBER (1904), VOIT (1909), TERRY (1917) and others agree with this opinion of GAUPP. According to TERRY even the occurrence of this caudad extension of the nasal capsule may be followed in the ontogeny of the cat. With regard



VOL
27
194

to the above it is of great interest that the paired condition occurs both in the subcerebral portion of the nasal septum and in the anterior part of the trabecular plate and that it extends rostrad almost to the limit between the praecerebral and subcerebral portions of the nasal capsule. If we now accept the conception of GAUPP, we have to regard the paired part of the nasal septum as corresponding to the interorbital septum of the Reptiles. In this group a paired interorbital septum has only been found in embryonic stages (in Chelonians, KUNKEL 1912, cf. also PEHRSON 1945, fig. 6). This implies that the adult occurrence of a paired interorbital septum must be sought in still much earlier phylogenetic stages. As DE BEER (1937) points out, the formation of an interorbital septum has occurred independently on numerous occasions in vertebrate evolution. As this structure does not exist in Rhipidista (Osteolepidoti), which among the Crossopterygii are said to be the ancestors of Tetrapoda, but is well developed in primitive Stegocephalian, it may be expected to have occurred paired in the adult skull somewhere in the evolutionary line between these two groups.

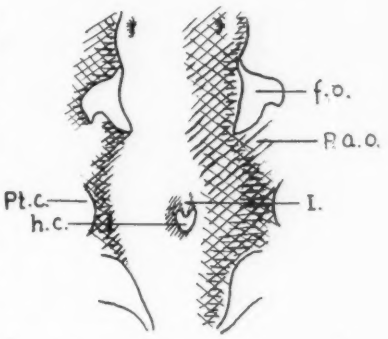


Fig. 3. *Procavia capensis*, 36 mm. embryo. Ventral view of the central stem in the orbitotemporal region. *f.o.* foramen opticum, *h.c.* hypophysial canal, *i.* intertrabecle, *p.a.o.* posterior root of ala orbitalis, *pt.c.* pterygoid cartilage. Reconstruction. 15 ×.

An ancient structure appearing in connection with the closure of the hypophysial canal has been observed in Procavia capensis.

In a 33 mm. embryo in which the first signs of ossification are to be found in the posterior portion of the basal plate and in the anterior portion of the Meckel's cartilage, the central stem of the orbitotemporal region is well chondrified. Between the processus alares its dorsal surface forms a wide fossa hypophyseos, which in its middle slopes downward, forming a funnelshaped canalis hypophyseos, filled with mesenchyme. Through this a hypophysial stalk with wide lumen descends. Ventral to the central stem it loses its lumen and bends craniad. Becoming finer and finer it finally disappears in the connective tissue.

In a 36 mm. embryo (fig. 3) the ala temporalis and the pterygoid cartilages have begun to ossify. In the former the ossification takes place from the perichondrium. The hypophysial stalk has a short lumen only in the wider part of the hypophysial canal, the rest showing the properties of a ligament. The canalis hypophyseos has become wider because of the growth of the surrounding cartilaginous masses. At the same time it has changed its form, being drawn out rostrocaudad. A high but rather short and thin sagittal

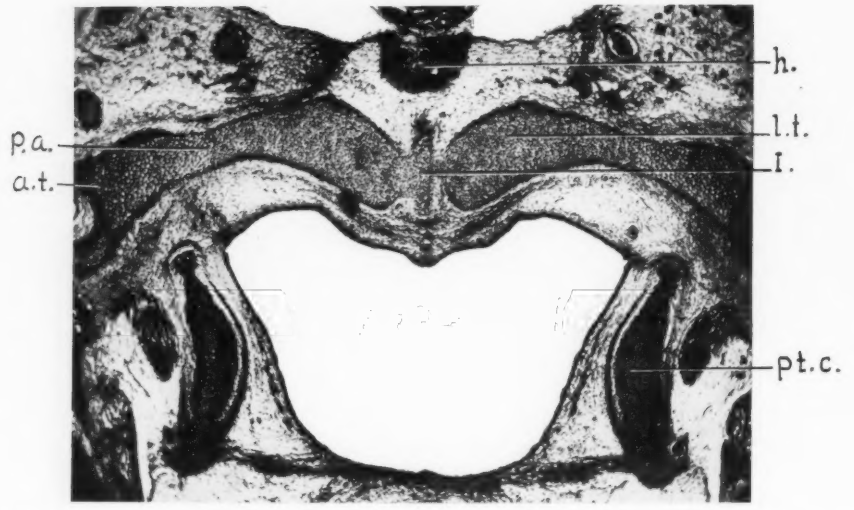


Fig. 4. *Procavia capensis*, 36 mm. embryo. Cross section through the anterior portion of the hypophysial canal. *a.t.* ala temporalis, *h.* hypophysis, *i.* intertrabecle, *l.t.* lamina trabecularis *p.a.* processus alaris, *pt.c.* pterygoid cartilage. 30 ×.

lamella of cartilage (fig. 4) is growing caudad from the anterior wall of the canal. Anterior to the free lamella the structure of the cartilage on both sides shows that a fusion has taken place and thus a part of the canalis hypophyseos has already been filled out by the lamella. Dorsad the latter extends into the fossa hypophyseos and can be followed craniad a short distance as a ridge which gradually becomes lower and broader. In front of this ridge the structure of the cartilage indicates that the most anterior part of the fossa hypophyseos has been filled out as far rostrad as to the tuberculum sellae with cartilage of the same kind as that forming the sagittal lamella. A corresponding ridge on the ventral surface of the central stem extends to the level of the tuberculum sellae.

In a 42 mm. embryo the periosteal ossification of the ala temporalis has spread to that portion of the central stem which is mainly caudal to the hypophysial canal. This has become compressed from the sides and is very narrow. The walls of its posterior portion are coated with periosteal bone and also an endochondral ossification is proceeding. The posterior, less narrow part of the hypophysial canal gives passage to two small veins and the hypophysial stalk, which, although lacking a lumen, is less reduced than in the 36 mm. embryo. No trace of the sagittal lamella with its two ridges can be discovered. Just anterior to the hypophysial canal, however, the cartilage shows three different zones: two broad lateral areas with the typical structure which precedes the endochondral ossification, and between these a median narrow



VOL 27 194

zone made up by young cartilage with small cavities. This median zone of cartilage perhaps corresponds to the sagittal lamella of the 36 mm. embryo.

From the preceding account it appears that the closure of the hypophysial canal takes place either before or after the ossification of the walls of the canal. If this process starts comparatively early the growth of the cartilage will be arrested. This may be the cause for the failure of the sagittal lamella to appear in the 42 mm. embryo.

When we deal with the morphological significance of the described cartilaginous lamella in the canalis hypophyseos, the only structure in the Sauropsida to be taken into consideration is the intertrabecula. This term is, however, used in two different senses, as has been emphasized by FUCHS (1915) and PEHRSON (1945).

1. PARKER (1880) investigating the development of Chelone mydas introduced the term and referred it to the cartilage between the rostral parts of the trabeculae. PEHRSON (1945), who inquires "if there is any ground for interpreting this portion of the septum interorbitale as an independent structure...", emphasizes that PARKER uses the term irrespective of whether the cartilage continues caudad to cross the fenestra basicranialis anterior. FILATOFF (1906) describing intertrabecles in Pristiurus, Emys and Columba, obviously uses, as pointed out by PEHRSON, the term in the sense of PARKER, as is also done to some extent by VERSLUYS (1936). PERHSON, after studying the development of three Chelonians (Dermochelys coriacea, Lepidochelis olivacea and Chrysemys marginata) arrives at the conclusion that an intertrabecle in PARKER's sense does not exist in forms (Dermochelis) where the anterior ends of the trabecles form a kind of "trabecula communis, leaving no space between them for any intertrabecular structure", whereas in such forms (Lepidochelis, Chrysemys) which do not develop a trabecula communis, an intertrabecula is formed. He considers this structure to be the developing interorbital septum and "that it might be discovered in other Chelonians as well, and even in other animals where no real trabecula communis forms". According to FUCHS (1915) the intertrabecle described by PARKER (1883) in crocodile embryos constitutes a portion of the interorbital septum.

2. The term has been applied in the other sence by NICK (1912), FUCHS (1915) and VERSLUYS (1936) to a sagittal cartilaginous bar dividing the fenestra hypophyseos into right and left halves. To avoid confusion with PARKER's intertrabecula, FUCHS (1910) proposed for this structure the name "taenia intertrabecularis, which has later been also used by DE BEER (1937) and PEHRSON (1945). As the "taenia intertrabecularis" at most can be regarded as an intertrabecle in a limited sense, I prefer to employ the former name in the following account.

The taenia intertrabecularis was first described by FUCHS (1910) in Chelonia

imbricata and has chiefly been studied in Chelonians, in which, however, there seem to be two types of taenia intertrabecularis with respect to development.

GAUPP (1905—1906) describes a Chelonia embryo — supposed by FUCHS (1915) to be a Chelonia mydas — in which the fenestra hypophyseos has been divided into one anterior and two posterior foramina. FUCHS (1910) assumes that in Chelonia imbricata the original fenestra hypophyseos has been divided by a cross bar into an anterior opening under the hypophysis and a posterior one which is then divided by a sagittal bar, the taenia intertrabecularis. In a later paper (1912) he has found that the fenestra basicranialis anterior will be first divided sagittally by the orad-growing taenia intertrabecularis, the cross bar being formed later. This opinion is maintained in his more detailed account (1915). In view of NICK's (1912) supposition that the taenia intertrabecularis is formed as a caudad prolongation of the ventral edge of the interorbital septum, FUCHS especially emphasizes the existence of the anterior opening which he calls foramen hypophyseos. Even here he is not quite sure that the sagittal bar develops before the transversal one. This is, however, strongly supported by his descriptions of the cartilaginous structure in the taenia and its connections with the trabecles (p. 100). The foramen hypophyseos will later be closed by the broadening of the trabecles.

The other type of formation of the taenia intertrabecularis has been described by PEHRSON (1945) in Lepidochelis. Here, as is seen in PEHRSON's fig. 12, the fenestra hypophyseos is considerably less caudorostrad extended and corresponds only to the openings for the carotid arteries, the hypophysis being situated anterior to the fenestra dorsally to a cartilaginous plate. This has been formed by the fusion of the trabecles, which process has obviously proceeded caudad without leaving an opening under the hypophysis. The taenia intertrabecularis develops chiefly as a large processus basisphenoidalis growing rostrad from the anterior edge of the basal plate and meeting an anterior short processus intertrabecularis, which arises from the anterior wall of the fenestra, i.e. the fused trabecles. On the basis of these results PEHRSON interprets the discontinuous "intertrabecle" described by NICK (1912) in a ripe embryo of Dermochelis as a developmental stage of the taenia and also rejects NICK's suggestion of the taenia intertrabecularis developing as a prolongation of the ventral posterior edge of the interorbital septum.

The taenia intertrabecularis appears, as pointed out by PEHRSON, comparatively late in the chelonian development.

As to the occurrence of intertrabecular structures in Reptiles other than Chelonian, some statements have been made. RATHKE (1839) describes in young stages of Coluber (Tropidonotus) natrix a structure which has been interpreted by VERSLUYS (1936) as being perhaps an intertrabecle. The existence of such a structure is, however, not confirmed by BÄCKSTRÖM (1931) in his thorough investigation of the development of this animal. PARKER's (1883)



VOL. 27 194

intertrabecle in crocodile embryos is referred to on p. 95. FUCHS reports a medial short cartilaginous process in a 5 ½ cm. crocodile embryo of unknown species situated on the anterior end of the basal plate, protruding into the fenestra hypophyseos and reaching just into the region of the caudal portion of the hypophysis. He interprets this process as being perhaps homologous with the posterior portion of the taenia intertrabecularis in the Cheloniidae. In PEHRSON's terminology it constitutes a processus basisphenoidalis. According to PEHRSON a short processus basisphenoidalis is to be found in an embryo (head length 12 mm.) of Crocodilus niloticus, whilst this structure is hardly to be discerned in an Alligator embryo (head length 17 mm.). In a full-time embryo of Passer domesticus DE BEER and BARRINGTON (cf. DE BEER 1937) have found a taenia intertrabecularis dividing the hypophysial fenestra into right and left halves.

Let us now return to the cartilaginous sagittal lamella in the hypophysial canal of Procavia. As this is situated anterior to the hypophysial stalk we are obviously dealing with an intertrabecle protruding caudad into the fenestra hypophyseos and thus representing the posterior edge of the interorbital septum. In one respect, however, this mammalian intertrabecle differs from that of the Chelonian. It appears very late in the ontogeny. It may, however, be detected, despite the presence of a "trabecula communis".

DE BEER (1937) points out that the taenia intertrabecularis is comparable as to position with the mammalian hypophysial plate. In placental mammals this develops as a central stem and may arise from paired centres of chondrification. The mode of junction between the hypophysial cartilage and the anterior end of the parachordal plate has not been very thoroughly studied. A fenestra basicranialis has been described in early mammalian embryos as lying between the hypophysial cartilage and the parachordal plate by NOORDENBOS (1905), TERRY (1917), FAWCETT (1917) and DE BEER and WOODGER (1930). NOORDENBOS, working on Talpa, performed his investigation on van Wijhe preparations. All histological details are thus lacking. TERRY finds in a 12 mm. embryo of Felis a small space between the hypophysial cartilage and the terminal expansion of the basal plate occupied by mesenchyme, the type of which is not more closely described. FAWCETT, dealing with a 25 mm. embryo of Microtus, writes: "The foramen through which the chorda-dorsalis passes is the remnant of a much larger one in the younger stages, and represents the gap between the pars chordalis and the pars trabecularis — in other words the basi-cranial fenestra of reptilia." According to DE BEER and WOODGER there is posterior to the hypophysial cartilage "a gradual transition into procartilage between the hypophysial plate and the parachordal plate, in such a way as to leave a small zone relatively free from any skeletogenous tissue. This zone corresponds to the fenestra basicranialis of other forms. Some of these statements are discussed by DE BEER (1937). I have studied,

with concordant results, the relevant stages of Procavia, Sus and Elephantulus and made the following observations. In early stages there is a small cartilaginous nucleus under the hypophysis and a cartilaginous rod corresponding to the posterior part of the parachordal plate and in between a gradual transition into procartilage and condensed mesenchyme, the whole gap between these two rudiments being filled with a more or less dense mass of skeletogenous tissue. In the parachordal plate the chondrification proceeds rostrad and the hypophysial cartilage extends caudad by a diffuse chondrification of the blastema until the two rudiments fuse anterior to the otical capsules. In none of these forms can there be question of a real fenestra as there are no distinct anterior and posterior boundaries, and the gap between the two rudiments is filled by skeletogenous tissue. In Erinaceus, however, some indications of the ancestral existence of a fenestra are found. This is of special interest in view of the very high geological age of the genus Erinaceus (cf. LECHE 1896). In an 11 mm. embryo the hypophysial plate and the parachordal plate are both chondrified, but leaving between them a space filled with condensed mesenchyme. There is, however, a remarkable difference between the anterior and the posterior borders of this space. Whereas in the former there is a gradual transition into cartilage and condensed mesenchyme, the anterior end of the parachordal plate shows a very well defined boundary covered with a sheet of flat cells. This boundary indicates a free surface of the anterior end of the parachordal plate in some ancestral form, constituting the posterior border of a fenestra basicranialis anterior. This fenestra does not, however, exist in the present embryo as it is filled with skeletogenous tissue. In a 15 mm. embryo the two rudiments have joined but the line of junction is still clearly seen. From its position it may be concluded that the anterior end of the parachordal plate has grown very little rostrad if at all, whilst the hypophysial cartilage has filled up the earlier space by a chondrification proceeding caudad. This implies that the relevant portion of the central stem is formed, in concordance with DE BEER's opinion, by the hypophysial cartilage. A comparison with the Chelonian taenia intertrabecularis reveals the great difference that whereas the latter is chiefly formed by a rudiment belonging to the parachordal plate, the portion of the central stem under consideration arises from a rudiment derived from the trabecles, comparable to a "processus intertrabecularis".

## SUMMARY.

1. A paired nasal septum has been observed in the subcerebral portion of the nasal capsule of a 21 mm. embryo of Sus domestica.

2. In a 36 mm. embryo of Procavia capensis an intertrabecle corresponding to the posterior edge of the interorbital septum was found protruding caudad into the hypophysial canal.



VOL
27
194

3. A real fenestra basicranialis anterior is formed neither in Procavia, Sus, Elephantulus, nor in Erinaceus. In the latter the anterior end of the parachordal plate shows a well defined boundary suggesting a posterior border of an ancestral fenestra basicranialis anterior. By caudad chondrification the hypophysial plate joins the anterior end of the parachordal plate. The formation of this part of the central stem is compared with that of the chelonian taenia intertrabecularis.

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VOL
27
194

# ON THE ARTERIES IN THE HEAD OF PROCAVIA CAPENSIS PALL. AND THEIR DEVELOPMENT

BY

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VOL.
27
1946

CONTENTS

Introduction . . . . . 101
Material and methods . . . . . 102
Observations . . . . . 103
4 mm embryo . . . . . 103
4·5 „ „ . . . . . 105
5·5 „ „ . . . . . 106
6 „ „ . . . . . 108
7·5 „ „ . . . . . 108
9 „ „ . . . . . 110
10 „ „ . . . . . 111
11 „ „ . . . . . 112
12 „ „ . . . . . 113
15·5 „ „ . . . . . 114
16·5 „ „ . . . . . 116
17 „ „ . . . . . 117
19 „ „ . . . . . 118
33 „ „ . . . . . 120
80 „ „ . . . . . 127
Previous observations on adult animals . . . . . 128

Discussion
Aortic arches . . . . . 130
Basilar artery . . . . . 138
Origin of the external carotid and the development of the stapedial artery . . . 140
On the arteria cerebri anterior . . . . . 143
Comparative morphology . . . . . 144

Summary . . . . . 149
Bibliography . . . . . 150
Explanation of letterings . . . . . 153

## INTRODUCTION.

The Hyracidae, appearing already in miocene, have preserved many archaic characters up to the present time. Nevertheless they still show a remarkable

vital activity exhibited in a great individual variation of the cranial bones and of the hair colour (JOLEAUD 1937). As they constitute a very primitive ungulate group the Hyracidae have attracted much attention. Anatomical descriptions (CUVIER 1804, MURIE and MIVART 1865, GEORGE 1874 and others) of these mammals appeared at an early stage and they were long placed in the vicinity of the Perissodactyla. COPE (1882) was the first to range the Hyracoidea together with the Proboscidea, and the near relationship between these two groups is emphasized by GREGORY (1910), ABEL (1928), WINGE (1942) and others. ABEL considers the Hyracidae to be most closely related to the extinct oligocenian Arsinotherium of El Faiyum (cf. JOLEAUD 1937).

Having a rather closely graded series of embryonic stages of Procavia capensis at their disposal the present authors found it tempting to study the development and the anatomy of the arterial system in the head of this primitive ungulate. As far as we have been able to establish, nothing is known about the development of the arterial system in this animal. In the adult Procavia capensis the circulatory organs were described by GEORGE (1874). Some complementary notes were added by BEDDARD (1904, 1909) who, in view of the location of the internal carotids "at the posterior end of the circle of Willis", regards Procavia to be closer to the Perissodactylae than to the Artiodactylae section of the Ungulates. Dealing with our older stages representing the conditions of the adult, we have worked out the descriptions in more detail for vessels only mentioned or erroneously described by preceding authors, and are somewhat brief with respect to those already treated closely. As the arteries providing the brain are very difficult to follow in their distal portions in our material and are already described, we shall confine ourselves to the description of their origins.

VOL.
27
194

## MATERIAL AND METHODS.

The embryos studied measured from 4 to 80 mm. To characterize the stage of development the body length, and in specimens from 10 mm body length the length of the head was determined. In smaller specimens, in which the measurement of the head length is very unreliable, the stage will be characterised not only by the body length but by some notes on the developmental stages of various organs. In the larger embryos the arteries will be portrayed with the outline of the chondrocranium (taken from a manuscript by the senior author) as background.

The embryos were fixed in Bouins fluid and preserved in 70 % alcohol. Up to 12 mm body length they were sectioned perpendicularly to that part of the brain between the cervical and the mesencephalic flexures. In larger specimens the plane of sectioning was chosen so as to form equal angles with

ventral surfaces of the anterior and posterior portions of the central stem of the chondrocranium, these two surfaces forming an obtuse angle. The thickness of the sections was varied with the size of the embryos:

| Body length in mm. | Thickness of sections in $\mu$ |
|---|---|
| 4 — 4.5 | 8 |
| 5.5—12 | 10 |
| 15.5—33 | 15 |
| 36 —42 | 20 |
| 60 | 30 |
| 80 | 40 |

OL.
27
946

The sections were stained with Azan-Mallory and the pictures needed for the graphic reconstructions were photographic negatives. The reconstructions of the 10, 11, 12, 15.5, 16, 19 and 33 mm embryos have been made by the junior author while the remainder of the reconstructions, with the exception of some details in the youngest stages (worked out by Mrs. S. THÖRNBLOM) and writing of the text have been performed by the senior. All the figures have been drawn by Mrs. S. THÖRNBLOM, to whom we express our thanks for her thorough work.

## OBSERVATIONS.

### 4 mm embryo (fig. 1).

The invagination of the optic vescicle has not yet commenced and the covering epidermis, slightly thickened, forms a lens placode. The mandibular processes are just on the point of fusing. The otocysts do not show any differentiations. The respiratory diverticulum of the fore gut has become bi-lobed. Three aortic arches can be recognized at this stage.

The truncus arteriosus (*tr.a.*) running caudodorsad enters an unpaired aortic sac (*a.s.*) from ventrad near the caudal border of the latter. The sac is dorsoventrally flattened and about as broad as it is long. Its anterior part is rostrolaterad extended into a common trunk for the first and second aortic arches. On the level of the rostral end of the otical vesicle this trunk constituting a short anterior ventral aorta divides into the two arches. One of these immediately runs laterad and, encircling the pharynx, fuses with the dorsal aorta forming the second aortic arch (*II*). The other one extends rostrad closely to the median plane imitating an anterior paired ventral aorta, enters into the mandibular arch, bends in front of the first pharyngeal pouch laterad and, encircling the pharynx, joins the dorsal aorta forming the first

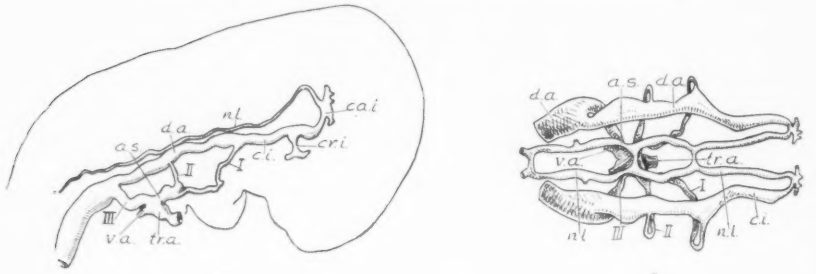



Fig 1. 4.0 mm embryo. *a* view from the right side of the arterial system. Reconstruction 20/1. *b* dorsal view of the arterial system. Reconstruction 20/1. The numerous lateral branches of the longitudinal neural arteries are not drawn.

aortic arch (*I*). From the caudal portion of the aortic sac springs on either side the third (*III*) aortic arch, which, taking a rather caudal course, is the greatest of the aortic arches in this stage. The caudal wall of the aortic sac shows a median shallow but pointed incision indicating a fusion of two lateral components. Between this incision and the ventral root of the third aortic arch there is a caudally directed protrusion on either side representing a rudiment of a posterior ventral aorta (*v.a.*). The dorsal aorta (*d.a.*) runs as arteria carotis interna craniad, and, branching dorsal to the stalk of the optic vesical, forms a ramus cranialis (*cr.i.*), which extends forward towards the anterior end of the cerebral hemispheres, and a ramus caudalis (*ca.i.*), which ventral to the cephalic flexure forms a large sinus-like extension. This gives off several small dorsally directed branches. Then the ramus caudalis turning caudally joins the longitudinal neural artery (*n.l.*). Approaching each other and then bending slightly to the side again the two internal carotids come into closest proximity on a level with the cranial end of the notochord.

The right and the left longitudinal neural arteries, (*n.l.*) which are somewhat irregularly shaped and sinus-like, extend almost parallel under the brain. They have no connections with any derivatives of the dorsal aortae until the anterior cervical region, where they join the intersegmental arteries of the third and the following cervical segments. Intersegmental arteries anterior to the third cervical one seem to be lacking. The neurals communicate with each other at three points through short vessels: on a level with the first aortic arch, ventral to the otic vesicles and near the hypoglossal roots. These are the primary longitudinal neurals, defined by their very intimate relationship with the surface of the brain, which they follow very closely, mesenchyme cells having squeezed themselves only at a few points between the vessels and the brain. In the region of the hypoglossus roots some small protrusions have been formed in the ventral wall of the longitudinal neural arteries. These buds extend longitudinally in their end parts, forming the rudiment of the secondary longitudinal neurals. The most caudal of the above-mentioned anastomoses between the right and



VOL 27 194

the left longitudinal neural arteries is formed by such rudiments and is separated from the brain surface by mesenchyme. The two cranial ones belong to the primary neural arteries and run much closer to the brain.

As the ramus caudalis of the internal carotid does not run close to the surface of the brain, the point at which the primary longitudinal neural artery runs into the ramus caudalis will be defined as that where the vessel loses contact with the brain surface. The longitudinal neural arteries give off numerous sinus-like branches which pass dorsad close to the sides of the hind brain.

### 4.5 mm embryo (fig. 2).

The invagination of the proximal part of the optic vesicles has begun and the lens placode forms a shallow pit. In the otocysts the rudiment of the endolymphatic sac appears. Six arches can be distinguished at this stage.

The aortic sac (*a.s.*) persists only between the two third arches. Its anterior portion has dissappeared together with the medial ventral part of the first (*I*) and second (*II*) aortic arches. From its anterior wall two blind protrusions extend rostrad near the median plane. They are probably the remnants of the

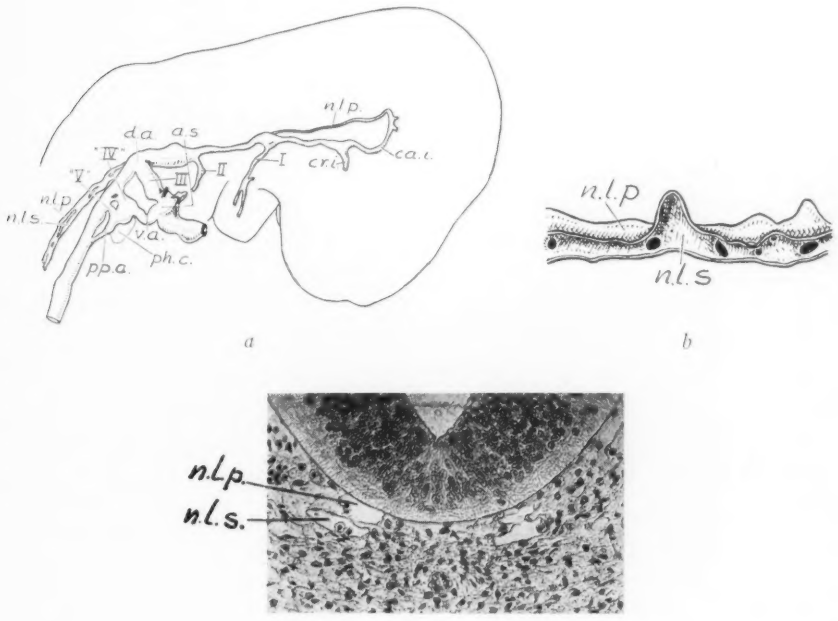



Fig. 2. 4.5 mm embryo. *a* view from the right side of the arterial system. Reconstruction 20/1. *b* detail of the longitudinal neural arteries from the side. The secondary neural artery cut open to show the anastomoses. Reconstruction 150/1. *c* crossection through the occipital region. 140/1.

anterior ventral aortae of the preceding stage. The ventral parts of the mandibular and hyoid arches are pierced by an extensively ramifying system of lacunae, which probably communicates with the two foremost aortic arches and also with the rudiments of the primary head and body veins.

The third aortic arch (*III*) is of considerable size and seems to represent the chief passage for the blood supply from the heart to the dorsal aorta. Just caudal to the ventral root of this arch a caudally directed trunk originates, constituting in its anterior portion a posterior paired ventral aorta (*v.a.*) and in its posterior portion a common ventral root of two arches, just to be described. It broadens and divides into two short arches, the anterior of which is situated rostral to the caudal pharyngeal complex enclosing a small isle, the posterior of which has a rostrolateral position to the caudal pharyngeal complex (*ph.c.*). We shall enumerate these arches as provisional fourth ("*IV*") and fifth ("*V*") arches. From the latter a trunk extends caudad lateral to the pouch. This must be considered as the *dorsal root* of a sixth arch which, however, gradually becoming rather thin, bends dorsad and joins the dorsal aorta. This connection with the dorsal aorta being not identical with the pulmonary arch and appearing before this will be termed *prepulmonary arch* (*pp.a.*).

The formation of the secondary longitudinal neural artery by junction of the buds described in the preceding stage and that of new buds have proceeded further rostrad, and this vessel now reaches from behind up to the second aortic arch, anterior to which new buds are formed by the primary vertebral artery. The secondary neural artery (*n.l.s.*) runs ventral and lateral to the primary (*n.l.p.*) one and in a short distance from the latter, to which it is connected by several anastomoses. The arrangement of these anastomoses is shown in more detail in fig. 2 *b* and *c*. The vessel connecting the neural arteries of the both sides near the second aortic arch is still formed by the primary vertebral arteries and consequently runs close to the brain surface.

### 5·5 mm embryo (fig. 3).

The optic vesicles are converted into cups and the lens placods are depressed to form deep pits. In the otic vesicles both endolymphatic sac and cochlear pouch can be distinguished.

Even here the anterior parts of the aortic sac (*a.s.*) are absent. By the fusion of the two caudal ventral aortae the aortic sac has extended caudad and is now very broad, connecting the third and fourth arches and joining the truncus arteriosus (*tr.a.*) posterior to the third arch. The two anterior aortic arches, which are relatively narrow, bend around the lateral parts of the pharynx and are ventral to this, connected by a wide, slightly branching lacuna. From the ventral remnant of the first arch a lacuna extends laterally to and along the mandibular division of the trigeminal nerve (*N.V.3.*). The provisional fourth



VOL 27 194

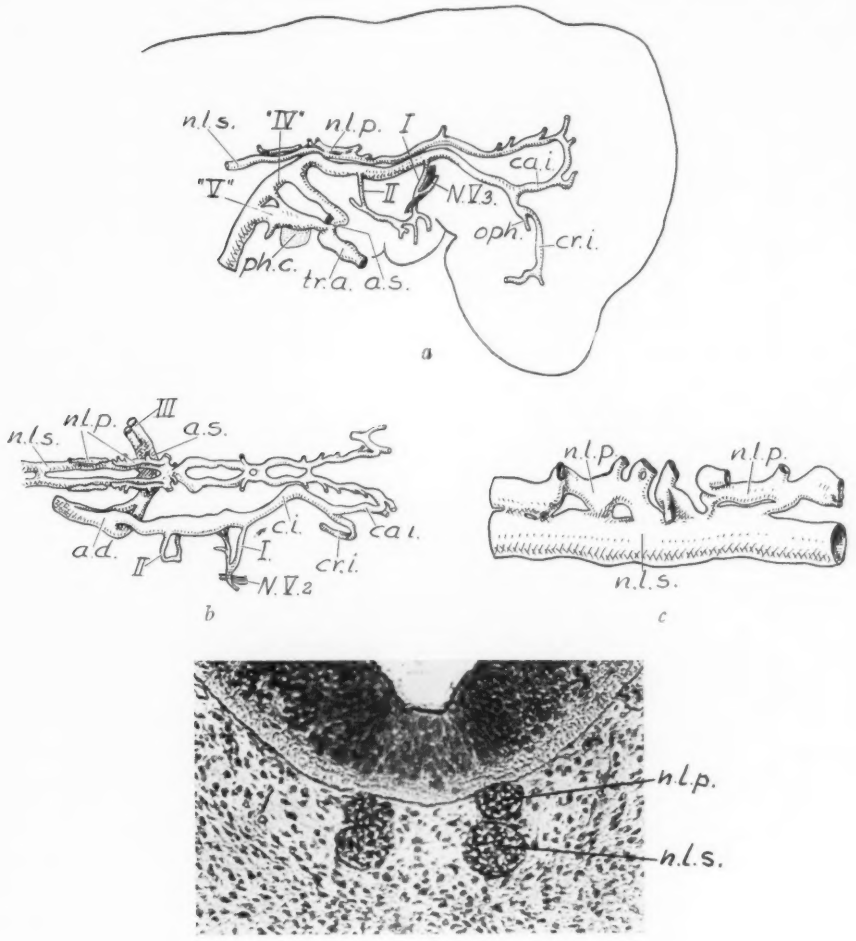



Fig 3. 5.5 mm embryo. *a* view from the right side of the arterial system. Reconstruction 20/1. *b* dorsal view of the arterial system. Truncus arteriosus omitted. Reconstruction 20/1. *c* detail of the longitudinal neural arteries from the side. Reconstruction 125/1. *d* crossection through the otical region 140/1.

("*IV*") arch, the reduction of which had already started in the preceding stage by the appearence of an isle, has become rather thin and the prepulmonary arch has been totally reduced. At the same time the common trunk of the provisional fourth and fifth ("*V*") arches has extended so that the blind stump, which is probably the remainder of the provisional sixth arch, is now situated posterior to the caudal pharyngeal complex (*ph.c.*). The caudal border of the aortic sac shows near the median plane two caudally directed outgrowths, the rudiments of the caudal ventral aortae.

Near its origin the ramus cranialis (*cr.i.*) of the internal carotid branches off an ophthalmic artery (*oph.*). The ramus caudalis (*ca.i.*) gives origin to a dorsally directed rudiment of a posterior cerebral artery and near its junction with the longitudinal neural artery a caudally directed rudiment of an anterior cerebellar artery.

The hindmost part of the primary longitudinal neural artery (*n.l.p.*) has begun to disintegrate, so that only short pieces remain (fig. 3 *c*). These are, however, still connected with the secondary neural artery by relatively long anastomoses, which give off vessels following the surface of the brain very closely. In the region of the second aortic to the pulmonary arches an almost continuous primary longitudinal neural artery still exists. Anterior to the second aortic arch the relationship between the primary and the secondary neural arteries is less clear. They run so close together and are so intimately fused, that often only the cross sectional form of the vessel indicates that similar conditions to those already described exist even here. A new anastomosis between the neurals of both sides has been formed anterior to the hypophysis. This anastomosis roughly marks the future anterior end of the basilar artery and is formed by the secondary longitudinal neural arteries.

VOL
27
194

## 6 mm embryo (fig. 4).

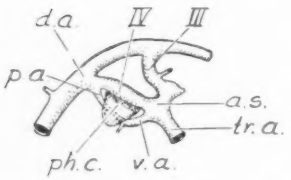



Fig. 4. 6 mm embryo. View from the right side of the posterior aortic arches. Reconstruction 20/1.

This embryo does not differ essentially from the preceding with regard to its developmental stage. Nevertheless some very important changes have taken place in the most posterior aortic arches. The definitive fourth aortic arch (*IV*) takes its ordinary place anterior to the caudal pharyngeal complex (*ph.c.*) which is here directed ventrally and somewhat caudally. As the provisional fourth arch has disappeared, the definitive fourth arch must be considered to consist of the common trunk of the provisional fourth and fifth arches and the provisional fifth arch. The caudal ventral aorta (*v.a.*) has grown out forming posterior to the ventral root of the pulmonary arch a short rudiment of the pulmonary artery. The pulmonary arch (*p.a.*) is a very narrow vessel originating from the dorsal root of the definitive fourth (the ventral end of the provisional fifth) aortic arch and running medially to the caudal pharyngeal complex.

## 7·5 mm embryo (fig. 5).

The lens vesicles are just closed but remain attached to the epidermis. An endolymphatic duct has been formed. The lung rudiments are inflated to

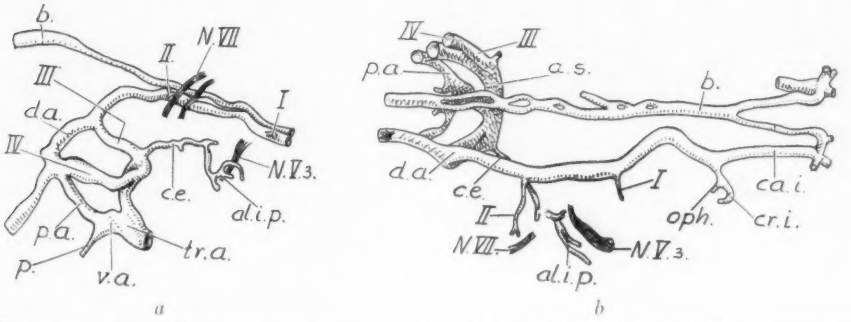



Fig. 5. 7.5 mm embryo. *a* view from the right side of the aortic arches. Reconstruction 20/1. *b* dorsal view of the arterial system. Truncus arteriosus omitted. Reconstruction 20/1.

vesicles. Owing to the sections in the anterior part of the head being damaged the lateral reconstruction could not be accomplished in this region.

From the rostrolateral wall of the ventral root of the third aortic arch (*III*) a newly formed artery originates. It constitutes the rudiment of the external carotid (*c.c.*). As the third arch will develop into the internal carotid, its root, now being common to both carotids, forms the rudiment of the common carotid. The external carotid approaches the dorsal aorta, and then bending still more laterad gives off a ventrally directed branch, which lateral to the ventral part of the mandibular division of the trigeminal nerve ramifies forming the rudiment of the arteria alveolaris inferior primaria. The fusion of the caudal ventral aortae has proceeded further caudad composing a posterior narrow prolongation of the aortic sac. Midway between the fourth (*IV*) and the pulmonary arches (*p.a.*) the truncus arteriosus (*tr.a.*) joins this prolongation and the still paired part of the caudal ventral aortae, which run out into the arteriae pulmonales propriae. These are still completely paired. As shown in fig. 4 the separation of the pulmonary trunk from the aortic trunk has just begun.

The ventral and lateral parts of the first and second aortic arches have disappeared and the lumina of the remaining stumps are very narrow. This stump of the second arch, being about twice as long as that of the first and extending laterad almost to the facial nerve, divides into two twigs, the caudal of which represents the arteria hyoidea of GRADENIGO (1887), the cranial the rudiment of arteria stapedialis. The fourth aortic and the pulmonary arches still have a dorsal common root. The former maintains its course medial to the ultimobranchial body.

Of the primary longitudinal neural arteries only very small remnants still occur. Here and there the original anastomosis between the secondary and primary neurals still remain as small dorsally directed twigs reaching from the former to the ventral surface of the brain, into which they often enter. All greater branches are given off by the secondary longitudinal neural artery and

run dorsad at a certain distance from the brain surface. The cranial parts of the neural arteries of both the sides have united, forming an unpaired basilar artery, whereas more caudal this process has not proceeded so far, the longitudinal neural arteries still being left piecemeal, enclosing several isles. As seen in fig. 5 *b* all parts of the longitudinal neuroral arteries do not contribute to the formation of the basilar artery. All parts of the longitudinal neural arteries and the basilar artery are separated from the brain surface by mesenchyme.

### 9 mm embryo (fig. 6).

The posterior lens cells have begun to elongate. The Jacobson organ appears as an epithelial thickening in the medial wall of the nasal pit. The arteriae pulmonales propriae have fused forming a single vessel.

The external carotid (*c.e.*) shows the same course as in the preceding stage, except that the arteria alveolaris inferior primaria (*al.i.p.*) has extended along the mandibular division of the trigeminal nerve (*N.V.3.*) lateral to this. The aortic trunk (*a.tr.*) is completely separated from the pulmonary trunk (*p.tr.*), the posterior part of which has arisen from the portion of the caudal ventral aortae between the truncus arteriosus and the pulmonary arch. As also the anterior portion of the pulmonary artery is now unpaired, the fusion of the caudal ventral aortae is thus accomplished. From the root of the first aortic arch a new vessel has developed. It runs lateroventrad to a point median to the proximal part of the mandibular branch of the trigeminal nerve. From here it passes rostrad and slightly mediad ventraly to the vena capitis lateralis but soon bends laterad to come into the vicinity of the maxillary branch of the trigeminal nerve (*N.V.2*), which it follows distally. This is the rudiment of ramus infraorbitalis of the stapedial artery (*i.o.s.*). The great superficial petrosal (Vidian) nerve (*N.p.*) follows the internal carotid to the point where this gives off the first arch. Here it bends rostrad running medially to the mentioned vessel (cf. fig. 6 *b* and *c*). The dorsal root of the second aortic arch has also become stronger. This branches medially to the facial nerve (*N.VII*), a short branch, the hyoid artery (*h.*), being directed caudally, while its main portion pierces the very diffuse mesenchymal condensation of stapes and extends forward ventrally to the vena capitis lateralis as the stapedial artery (*st.*). At the cranial end of the otic vesicle it suddenly bends ventrad approaching the mandibular ramus of the trigeminal nerve, which it follows distally over a short distance. Its end-part pointing to the dorsal end of the arteria alveolaris inferior primitiva constitutes the ramus inferior (*i.*) whith a small knot directed towards the future ramus infraorbitalis suggesting the point of fusion. Dorsal to this is a somewhat larger protrusion, the ramus superior (*s.*) of the stapedial artery.—The fourth aortic and the pulmonary arches are considerably smaller on the right than on the left side.



VOL.
27
1946

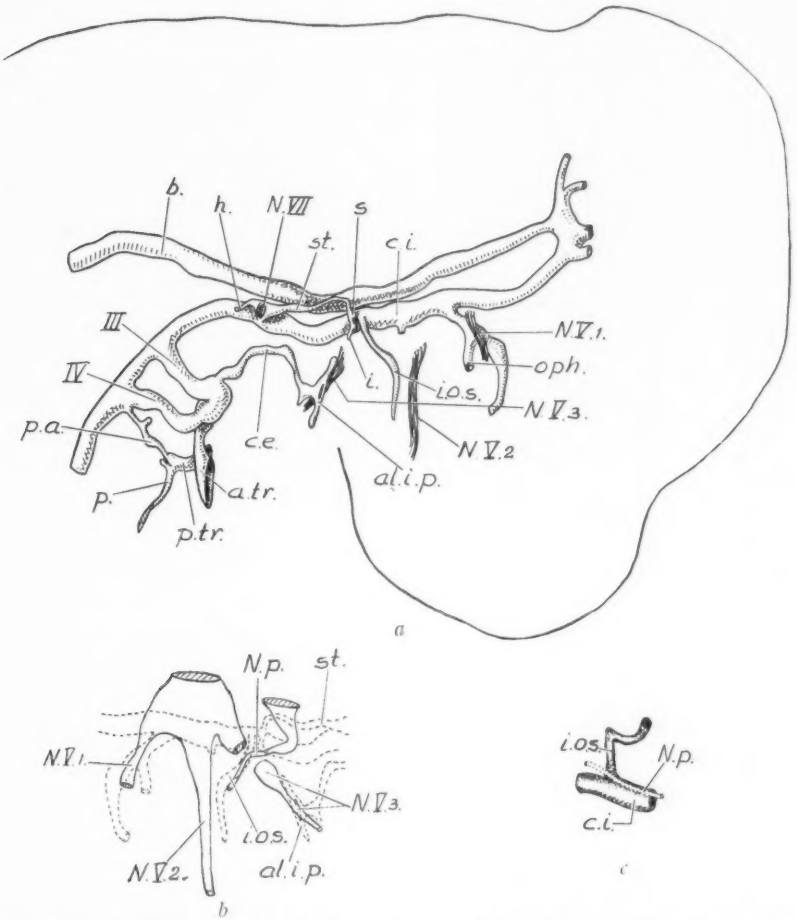



Fig. 6. 9 mm embryo. *a* view from the right side of the arterial system. Reconstruction 20/1. *b* detail of the trigeminal and facial ganglions with nerves and vessels (pointed) from the left side. Reconstruction 20/1. *c* detail of carotis interna with ramus infraorbitalis from ventral showing the relation of the latter to nervus petrosus superficialis major. Reconstruction 20/1.

The basilar artery (*b.*), being now unpaired in its total length, extends craniad to the cephalic flexure, where it joins the ramus caudalis of both the internal carotids. The basilar artery, unlike that of earlier stages or its equivalents, does not to any extent run between but mediodorsal to the two dorsal aortae.

### 10 mm embryo, head length 5 mm (fig. 7).

The primitive posterior nares are still not formed. The first centres of chondrification appear in the basal plate of the skull.

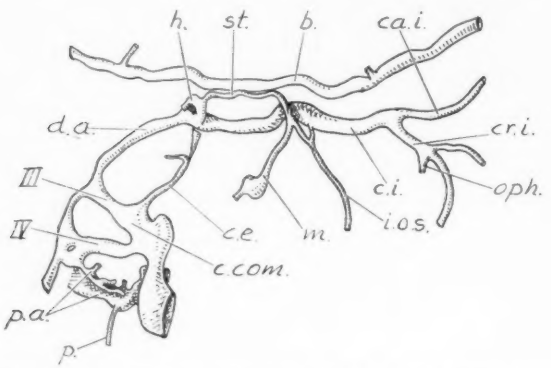



Fig. 7. 10 mm embryo. View from the right side of the arterial system. Reconstruction 20/1.

The external carotid (*c.e.*) has lost its connection with the arteria alveolaris inferior primaria, its descending extension in the lower jaw being reduced. Instead a new lateral rudiment continues its main direction extending to a point lateroventral to the stapes blastema. In the territory of the two foremost aortic arches several changes have taken place. The stapedial artery (*st.*) has fused with its ramus infraorbitalis (*i.o.s.*), which is still connected with the internal carotid by a small anastomosis, being the first aortic arch. The proximal end of arteria alveolaris inferior primaria has joined the ramus inferior, forming together arteria alveolaris inferior secondaria or the ramus mandibularis (*m.*) of arteria stapedia. A very small ramus superior is present. The hyostapedial trunk (BROMAN 1899) has changed its course. Running laterally in the preceding stage it here sets off from the internal carotid in a slightly dorsal direction. It then forks and the anterior branch enters into the very diffuse stapes blastema and extends forward. The ventral root of the third aortic arch has elongated and forms a short and very large common carotid (*c.com.*). The fourth aortic arch and the pulmonary arch still have a common dorsal root. The pulmonary arch (*p.a.*) on the right side shows signs of being reduced and the same is true of ductus caroticus, i.e. the portion of the dorsal aorta extending between the third and fourth aortic arches. The basilar artery extends in a plane which is definitely more dorsally situated than that of the internal carotids.

### 11 mm embryo, head length 5.5 mm.

The primitive posterior nares are formed. The tractus opticus is still hollow.

This embryo differs little from the preceding, the difference consisting mainly in the presence of a short arteria lingualis originating from the external carotid and forming together with its partner a short unpaired vessel, which extends ventral into the tongue. The common carotid has extended consider-



VOL
27
194

ably as has the very thin ductus caroticus. An aortic sac uniting the roots of the third and fourth aortic arches still exists but has grown relatively much less broad. A ramus superior of the stapedial artery is lacking.

### 12 mm embryo, head length 6 mm (fig. 8).

The tractus opticus is solid. The chondrification of the basal plate has proceeded so as to make it consist of young cartilage from the level of the still undivided internal auditory meatus to the foramen magnum, the cartilage tissue extending into the pilae occipitales.

The main trunk of the external carotid (*c.c.*) has lengthened considerably. It branches off the lingual artery (*l.*), passes laterally to the rudiment of the proximal part of the hyoid and extends almost to a point lateral to the extensively reduced arteria hyoidea, which forms a short caudally directed twig. Its distal part constitutes the rudiment of the ramus externus. The formerly straight part of the stapedial artery (*St.*) now makes a smooth dorsally convex curve. The anastomosis between ramus infraorbitalis (*i.o.s.*) and the internal carotid representing the first aortic arch has disappeared. Immediately behind the branching of the stapedial artery into the ramus infraorbitalis and the ramus mandibularis (*m.*) it gives off a short dorsally directed twig representing

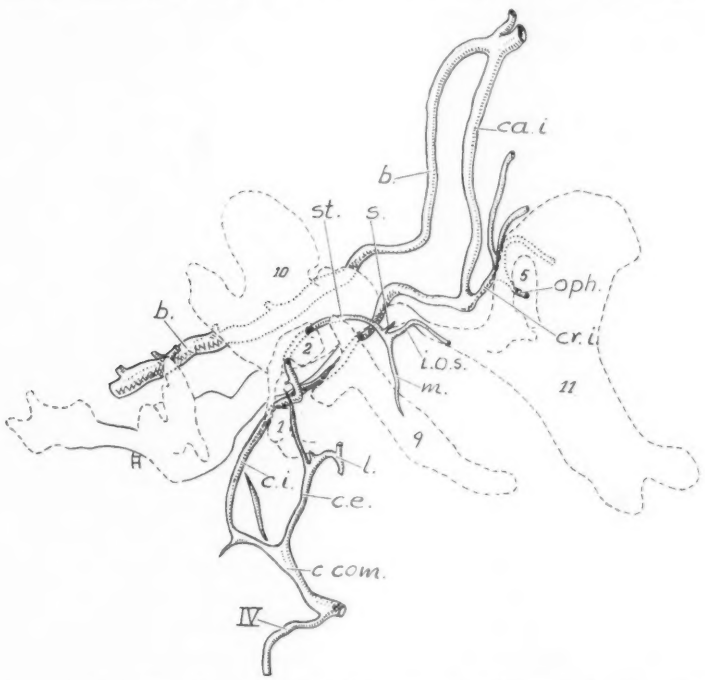



Fig. 8. 12 mm embryo. View from the right side of the arterial system. Reconstruction 20/1.

a ramus superior (*s.*). In the angle between the external and the internal carotids, but without connection with any of them, a rudiment of an artery has been formed running dorsolaterad, first along the vagus nerve and then laterally to the vena capitis lateralis. Ductus caroticus has dissappeared and may be traced only as a short caudally directed twig on the third aortic arch. The fourth arch of the right side is much smaller than that of the left. The ramus cranialis of the internal carotid, after having given off the ophthalmic artery, runs rostrally and branches off three vessels to the lateral surface of the hemisphere. Because of the development of the skeletal blastema in the basal plate and the auditory capsula the basilar artery has been still more detached from the internal carotids.

### 15.5 mm embryo, head length 7 mm (fig. 9).

In the complex of the external carotid (*c.e.*) no greater changes have taken place, only the angle between its distal part and the lingual artery (*l.*) having been enlarged, the former directing itself more ventrally, the latter more dorsally. This embryo shows an abnormality, the stapedial artery (*St.*) taking its origin not from the internal carotid (*c.i.*), but from the external one close to the branching of arteria carotis communis (*c.com.*). Hence the stapedial artery runs dorsad and laterad passing caudally to the dorsal end of Reichert's cartilage, bends rostrad and soon follows its normal course. No traces of the hyo-stapedial trunk on the internal carotids can be detected. The ramus infraorbitalis shows just anterior to the blastema of the ala temporalis a short lateral offshoot, the rudiment of the ramus orbitalis with arteria buccinatoria. The differentiation of the mesenchyme enveloping the brain has proceeded so far, that the rudiment of the dura mater may be distinguished. The internal carotid enters into this membrane in front of the otic capsule and, continuing its course in the membrane, branches cranially to the alar process into the cranial and caudal ramus, which both immediately extend inside the dura mater. The ramus cranialis of the interior carotid gives off three branches to the lateral surface of the hemisphere, one caudal to the pila postoptica, one caudal to the posterior border of the fenestra olfactoria, and one, the future arteria cerebri media (*c.m.*) between these two. Moreover, the ophthalmic artery (*oph.*) branches off medially to the pila postoptica and, bending ventrolaterad, passes through the optic foramen. At the posterior border of fenestra olfactoria the cranial ramus of the internal carotid divides into two branches, which, running forward together, first approach the septum nasi. The dorsomedial of these vessels is the anterior cerebral artery (*c.a.*) while the ventrolateral one constitutes a ramus ethmoidalis (*et.*). The two anterior cerebral arteries being just engaged in the formation of an arteria cerebralis anterior communis, each gives off two small medially directed branches, which



VOL
27
194

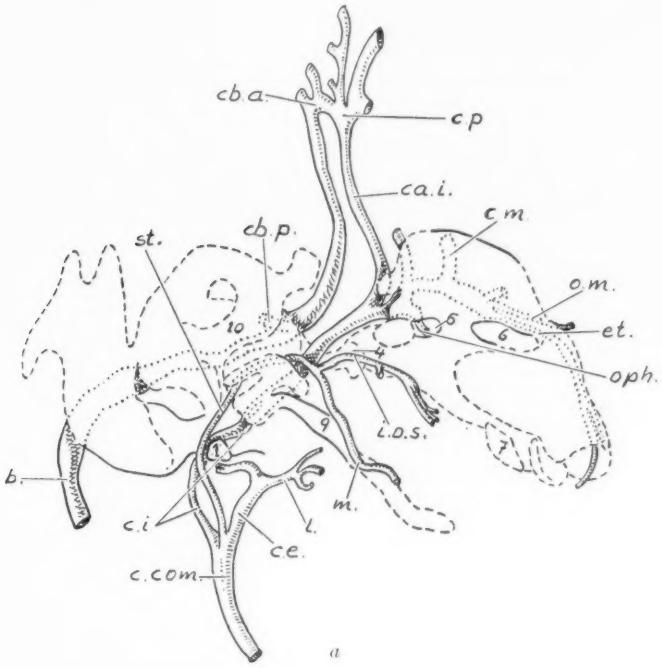
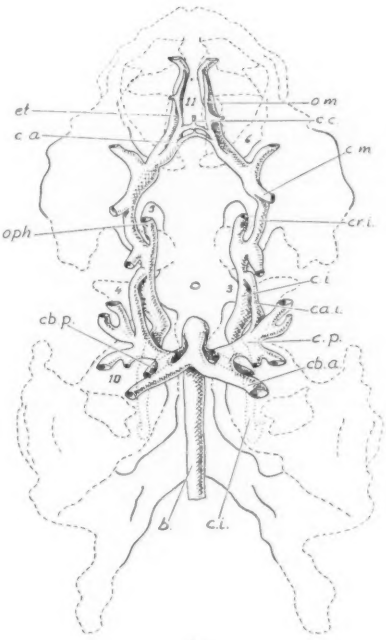



Fig. 9. 15.5 mm embryo. *a* view from the right side of the arterial system. Reconstruction 15/1. *b* dorsal view of the arterial system. Reconstruction 15/1.




pass into the fissura longitudinalis and join their partners of the other side. The posterior pair forms a small, short cranially directed twig, which runs into a larger likewise cranially directed artery, formed by the anterior pair and following the longitudinal fissure as a rudiment of arteria cerebralis anterior communis. We refer to these anastomoses as primary ones. A lateral branch of the arteria cerebralis anterior extends rostrad, running dorsal to ramus ethmoidalis. It gives off branches to the ethmoidal rete, in its posterior part a branch to the median surface of the hemisphere and further an anastomosis to the anterior part of ramus ethmoidalis. It subsequently bends

dorsad, passes between the bulbi olfactorii and penetrates into the medial surface of the lobus olfactorius. Although we cannot trace this vessel into the bulbus olfactorius, its general course indicates its identity with the arteria bulbi olfactorii medialis (*o.m.*) of the horse (HOFMANN 1900). The ramus ethmoidalis about at the centre of the fenestra olfactoria gives off several small arteries, forming the rudiment of a rete ethmoidalis, which has a connection, although very small, through fissura orbitonasalis with one of the branches of arteria ophthalmica in the orbit (a. ethmoidea externa). Near the anterior border of fenestra olfactoria the two rami ethmoidales come nearest to each other to diverge again immediately. At this point a small lacuna filled with erythrocytes is found between them, constituting the first rudiment of arteria ethmoidalis communis. The diverging part of ramus ethmoidalis gives off a branch to the bulbus olfactorius, which we will call arteria bulbi olfactorii anterior, and thereafter enters into the nasal cavity.

The ramus caudalis of the internal carotid has taken a more dorsal direction, the angle between the two rami being wider. Ventral to the flexure of the brain it gives off an arteria cerebri posterior (*c.p.*) and an arteria cerebellaris anterior (*cb.a.*) which soon branches. A posterior cerebellar artery (*cb.p.*) branches off from the basilar artery near the cranial end of the otic capsule, and, passing the internal auditive meatus, gives off a branch, which enters into the interior of the otic capsule.

### 16.5 mm embryo, head length 8 mm (fig. 10).

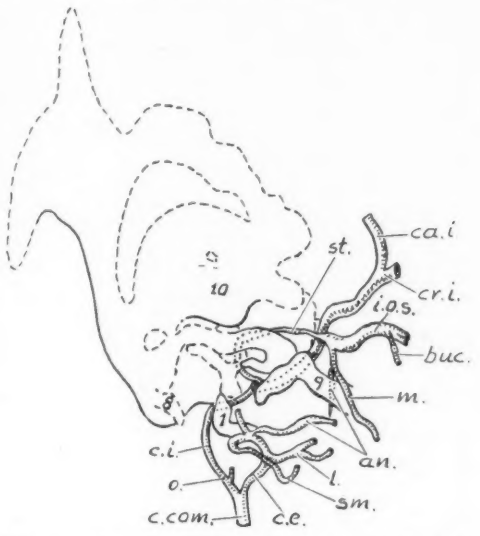
In this stage the rudiment of the anastomosis (*an.*) connecting ramus mandibularis (*m.*) with the system of the external carotid has appeared. It consists of two parts, one of which with its narrow caudal end joins the external carotid (*c.c.*), where this passes laterally to Reichert's cartilage. From here it extends craniad, becoming increasingly wider until it ends almost medially to Meckel's cartilage. With this rudiment the other forms an almost right angle. Its ventral narrow end just reaches the cranial end of the first mentioned rudiment and runs from here medially to Meckel's cartilage towards the branching of the stapedial artery. It reaches neither this point nor the ramus mandibularis, to which it comes quite near. In this embryo no traces of a ramus superior can be discovered in the stapedial artery the rostrad part of which has become rather thin. The ramus infraorbitalis, having just passed the lateral blastemal part of ala temporalis, gives off a laterally directed short branch, which constitutes the rudiment of the ramus orbitalis with the arteria buccinatoria. The external carotid has developed a new branch, constituting the rudiment of arteria maxillaris externa.

From the rostral wall of the internal carotid near its origin a small artery with thick walls can be followed a short distance laterodorsal towards the rudiment of the digastric muscle. It probably represents a rudiment of the root



VOL
27
194

of the occipital artery. The arteriae cerebrales anteriores converge more than in the preceding embryo. They are still joined by two pairs of primary anastomoses, the hindmost of which has become much wider. From there a pair of ventral secondary anastomoses are given off, joining medially. Arteria bulbi olfactorii medialis is totally missing; the only vessel supplying the most rostral parts of the brain is ramus ethmoidalis. An arteria ethmoidalis communis has so far not been formed.—The basilar artery extends caudad as far as the axis, where it bifurcates.




Fif. 10. 16.5 mm embryo. View from the right side of the caudal portion of the arterial system. Reconstruction 15/1.

17 mm embryo, head length 7.5 mm (fig. 11).

The connection between the external carotid system and the stapedial system is now accomplished. The anastomosis has joined the initial main trunk of the external carotid almost in the middle between the origin of the lingual artery (*l.*) and the branching of the initial trunk. This means a secondary displacement toward the lingual artery of the point of fusion in relation to that in the 16.5 mm embryo. The other end of the anastomosis has joined the ramus mandibularis (*m.*) of the stapedial artery (*st.*) at a certain distance from the ramification of the latter. Thus a piece of ramus mandibularis, the remainder of which is now called arteria alveolaris inferior, has been added to ramus infraorbitalis, both forming arteria maxillaris interna. In this portion the blood stream flows in the opposite direction to that before, since the stapedial artery has lost its lumen both caudal and rostral to the stapes and can only be traced as a very thin ligament. A short ramus superior (*s.*) can also be recognized in this embryo. The newly formed anastomosis between ramus mandibularis and carotis externa substitutes a ramus internus of the external carotid and the distal part of the original trunk of carotis externa a ramus externus of the latter, which here branches into the rudiments of the great auricular (*au.*) and the external maxillary arteries (*mx.e.*).

From the caudal wall of the external carotid and near the origin of the latter a small artery is given off. It first runs dorsad passing rostrally to the

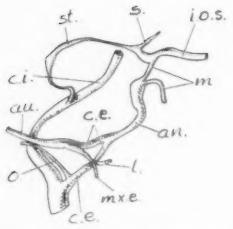



Fig. 11. 17.5 mm embryo. View from the right side of the caudal portion of the arterial system. Reconstruction 15/1.

internal carotid, than gradually bends laterad, passing caudally to the glossopharyngeal nerve and ventrally to the internal jugular vein, the ventrolateral surface of which it closely follows. It thus passes dorsad laterally to the internal carotid and comes near the cranial end of processus paracondyloideus, medially to which runs the above-mentioned vein. This artery, which cannot be traced any further, constitutes the rudiment of the arteria occipitalis (*o.*). Another rudiment of this vessel can be followed as a small artery extending between the caudal surface of processus paracondyloideus and the cranial mouth of foramen transversarium of the atlas.

The primary connections between the two anterior cerebral arteries have become reduced to one running out into the arteria cerebralis anterior communis, whereas there have been formed two new secondary anastomoses, which are medially connected by an arteria cerebri anterior communis ventralis. This embryo, contrary to that of 16.5 mm, shows considerable remnants of arteria bulbi olfactorii medialis, which, however, has lost on both sides its connection with ramus ethmoidalis. This remnant has its greatest extension on the right side.—Any connection between the rete ethmoidalis and the arteries of the orbita cannot be traced further.—The pair of third rami spinales of the vertebral arteries enters the vertebral canal between the third vertebra and the axis and both rami join each other and the basilar artery in the caudal part of the atlas.

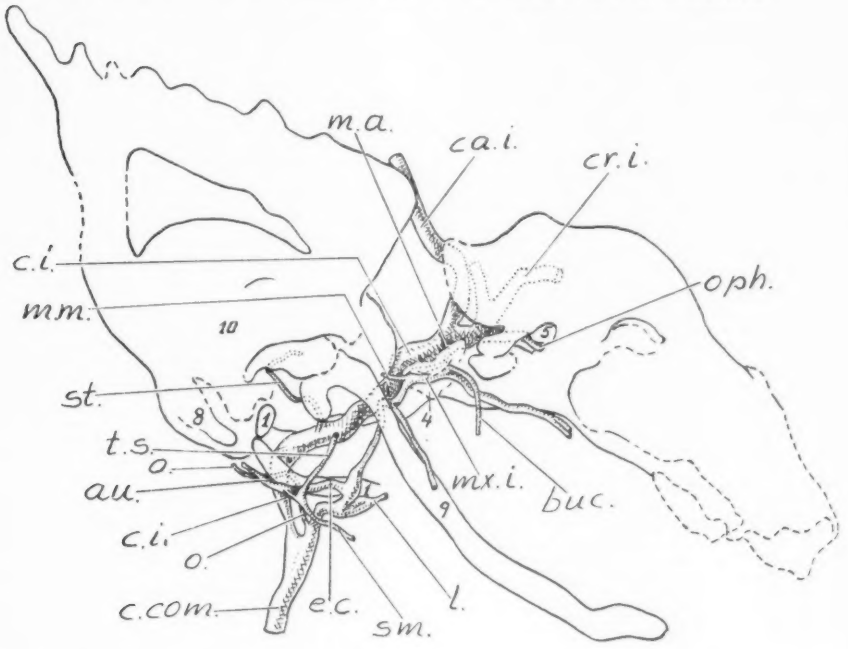
### 19 mm embryo, head length 10 mm (fig. 12).

Even in this stage the occipital (*o.*) artery originates from the caudal wall of the external carotid. It takes the same course as in the preceding embryo, but can here be traced further. It passes laterally to vena jugularis interna, i.e. between this vein and the rudiment of the tendon common to the digastric and stylohyoid muscles,[1] and follows this rudiment caudad to the anterior end of the paracondyloid process, to which it runs medially. In its further course only its ramus muscularis can be found. The three branches of the ramus externus (*e.c.*) of the external carotid are all developed for the first time. Arteria auricularis magna (*au.*) forms the prolongation of this ramus, whilst the superficial temporal (*t.s.*) and the external maxillary arteries (*mx.i.*) are given off by a short rostroventrally directed trunk. A rudiment of the anterior arteria meningea media (*m.a.*) has appeared and is given off by the internal maxillary artery (*mx.i*), where this branches off the ramus orbitalis.

[1] See the critical remarks of GEORGE (1874) on MECKEL's, MURIE and MIVART's descriptions of the stylohyoid muscle.



VOL
27
194



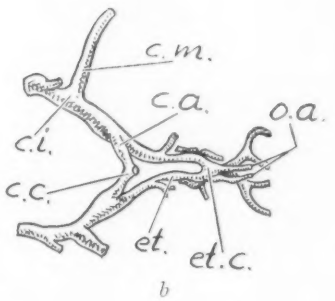




Fig. 12. 19 mm embryo. *a* view from the right side of the arterial system. Reconstruction 15/1. *b* dorsal view of ramus cranialis of the internal carotid. Reconstruction 15/1.

The distal part of the stapedial artery, i.e. that following the passage through the stapes, has totally disappeared and the rest of this artery (*st.*) has become very small. This embryo shows the ramus superior of the stapedial artery as a dorsally directed small artery originating from the internal maxillary artery, just where this bends rostrad. The ramus superior constitutes a rudiment of an arteria meningea media (*m.m.*), which enters into the otic ganglion. In the most rostral branches of the internal carotid (*c.i.*) more definite conditions have been established. The complicated junction between the two anterior cerebral arteries (*c.a.*) has been transformed into a simple one extending in an arteria cerebri anterior communis (*c.c.*). The secondary anastomosis as well as the arteria cerebralis anterior communis ventralis have disappeared. Arteria bulbi olfactorii medialis is totally missing. A short arteria ethmodalis communis (*et.c.*) uniting the anterior parts of the two rami ethmoidales has been formed. It gives off small subdural vessels and from its anterior end a paired dorsad-running branch, arteria bulbi olfactorii anterior (*o.a.*), which

furnishes the olfactory bulb as well as lobus frontalis. These branches are rather asymmetrical, one being situated medially whereas the other takes a lateral position as a prolongation of the right ramus ethmoidalis. The two rami ethmoidales part again and enter through the most cranial part of fenestra olfactoria into the nasal cavity, where they immediately fork into a medial and a lateral branch. Half way between its origin and its running into the arteria ethmoidalis communis, ramus ethmoidalis gives off a laterally directed branch.

The relations between the vertebral and the basilar arteries are somewhat irregular. The fourth pair of rami spinales, being rather small, enter the vertebral canal between the third and fourth vertebrae and join each other ventral to the cord. The resulting trunk, running somewhat to the right as the equivalent of the right third ramus spinalis, joins the corresponding great left vessel, which passes into the vertebral canal between the second and third vertebrae. The basilar artery near its posterior end gives off the small arteria spinalis ventralis.

VOL
27
194

### 33 mm embryo, head length 14 mm (fig. 13).

In this stage the arteries of the head correspond well with those under adult conditions as represented by a 80 mm embryo. The slight divergences will be briefly demonstrated after the description of this embryo. Some vessels, showing a great variation in their appearance, are described also in specimens of 36, 42 and 60 mm body length.

The bifurcation of the common carotid (*c.com.*) into the external and internal carotids takes place on a level with the cranial end of the paracondyloid process lateral to musculus rectus capitis anticus major and medial to the digastric and stylohyoid muscles. Between the external (*c.e.*) and internal (*c.i.*) carotids the hyoid protrudes rostrad. Near the bifurcation of the common carotid this gives off the arteria thyreo-laryngea (*t.-l.*) from its medial wall which extends a short distance rostrad, bends sharply caudad and runs in this direction ventral to the common carotid, providing thyreoidea, oesophagus, larynx and laryngeal muscles.

I. The external carotid gives off near its origin the lingual artery (*l.*), runs craniad a short distance and bifurcates lateral to the hyoid into two branches of about equal size, one of which forms a dorsolaterally directed ramus externus (*e.e.*) while the other continues craniad as ramus internus.

A. The lingual artery has been considerably displaced towards the root of the external carotid, now originating almost from the common carotid. It runs rostrad to the tongue.

B. Ramus externus follows the hyoid proximally, at first close to the lateroventral surface of the latter, then leaving this and proceeding laterally to the hyoid. It thus extends laterocaudad and branches rostrolateral to the

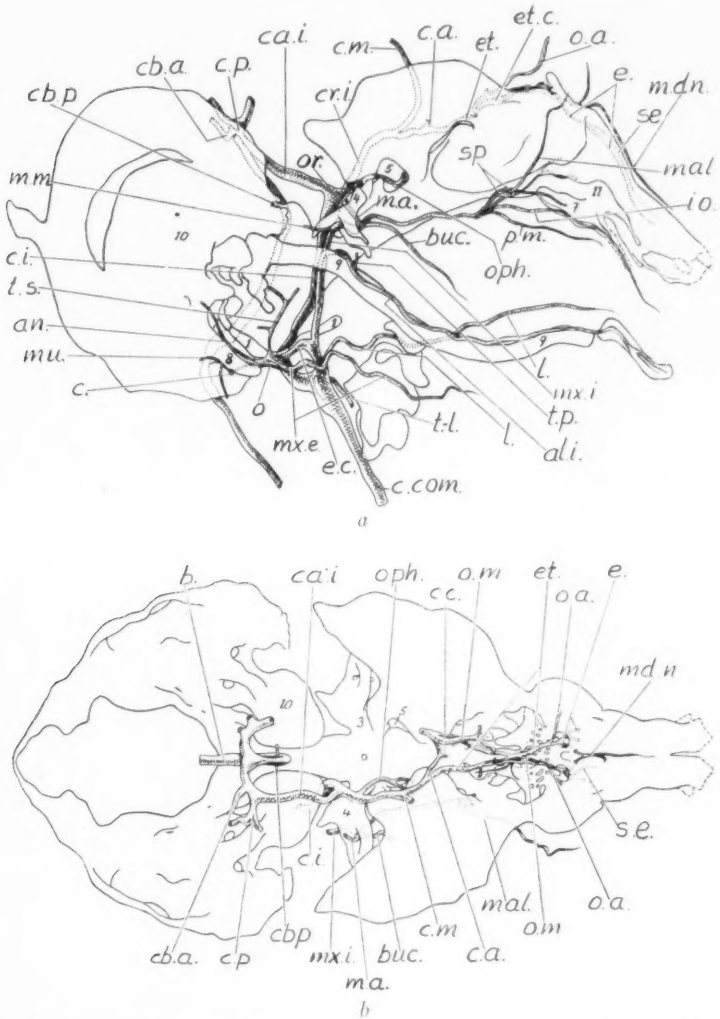



Fig. 13. 33 mm embryo. *a* view from the right side of the arterial system. Reconstruction 7.5/1. *b* dorsal view of the arterial system. Reconstruction 7.5/1.

end of the paracondyloid process. In this specimen its three branches, arteria maxillaris externa (*mx.e.*), arteria temporalis superfacialis (*t.s.*) and arteria auricularis magna (*au.*), originate from the same point.

Arteria maxillaris externa runs rostrad ventral to the ventral edge of the rudiment of the dentale, giving off branches to the submaxillary gland, musculus masseter and musculus pterygorideus internus. It gradually turns medial to the digastric muscle and extends rostrad medial to the ventral border of the anterior part of the jaw, giving off branches to the myleohoid muscle.

The arteria temporalis superficialis extends in the cranial direction caudal to the posterior border of the lower jaw. An anterior branch passes over the lateral surface of ramus articularis of the lower jaw and of the jugal bow, a posterior one over the squamosal, both furnishing the temporalis muscle and the skin. A caudally directed third extends to the area cranial to the meatus auditivus externus.

Arteria auricularis magna follows the dorsolateral border of the paracondyloid process, divides at the base of the said process into a caudal branch for the external ear and a cranial one, spreading its twigs laterally to the pars canalicularis of the otical capsule.—Thus the ramus externus of the external carotid chiefly supplies superficial parts with blood.

C. The ramus internus of the external carotid extends craniad medially to the lower jaw and the pterygoid muscles. On a level with the ventral border of Meckel's cartilage it gives off the inferior alveolar artery (*al.i.*) and, continuing in the same direction, is called arteria maxillaris interna (*mx.i.*). This runs medially to the ramus mandibularis of the trigeminal nerve, and arriving at a point caudal to the ala temporalis, simultaneously bends rostrad giving off a dorsally directed arteria meningea media (*m.m.*). It passes through the fissura alisphenoidea and then immediately branches off a ramus orbitalis to the side. Proceeding rostrad through the ventromedial part of the orbit the internal maxillary artery bifurcates about half way between the anterior and posterior borders of this cavity. Its two rami bifurcate again, thus giving rise to four branches, from medially laterad: arteria palatina major (*p.m.*), arteria sphenopalatina (*sp.*), arteria infraorbitalis (*io.*) and ramus malaris (*ma.*). Neither in this stage nor in the 80 mm embryo does the internal maxillary artery show the rete mirabile first described by HYRTL (1852).

Arteria alveolaris inferior bends near its origin round Meckel's cartilage and runs then laterally to this. Just on its arrival at the lateral side of the cartilage it gives off a small laterodorsally directed arteria temporalis profunda (*t.p.*), which furnishes the temporal muscle. This vessel has the same origin in the 36 mm embryo and also in one of 60 mm body length. In the 42 mm embryo, on the other hand, arteria temporalis profunda originates from arteria maxillaris interna some distance anterior to the flexure of the latter.

The arteria meningea media (*m.m.*) running dorsad pierces the otic ganglion, which the internal maxillary artery contacts when just bending. It then turns slightly craniad and enters the cavum supracochleare dorsal to the cartilage, which completes the foramen faciale secundarium. Here it ramifies, chiefly furnishing the dura mater. In the 36 mm embryo the arteria meningea media is totally lacking, but this is very well developed in the embryo of 42 mm body length. Here it originates from the ramus internus of the internal carotid just cranial to the branching off of the inferior alveolar artery. It extends craniad



VOL 27 194

medially to ramus mandibularis of the trigeminal nerve and divides between this and ganglion oticus into two branches. One of these proceeds in the same direction entering the skull cavity through the foramen ovale and ramifying in the dura mater. The other runs caudad into the otic ganglion and then enters the cranial cavity through foramen lacerum anterius taking the same course as arteria meningea media in the 33 mm embryo.

The short ramus orbitalis (*or.*) runs craniolaterad into the orbit, with the arteries of which it has no connections. It divides into a wide branch, arteria buccinatoria (*buc.*), extending in the same direction and a small anterior arteria meningea media (*m.a.*) which, directed cranially, passes through the foramen rotundum lateral to the maxillary division of the trigeminal nerve into the skull cavity, where it ramifies into the dura mater. This vessel, which seems never to be lacking, shows the same behaviour in the embryos of 36 and 80 mm body length. In the 42 mm embryo it originates from the internal maxillary artery at the same point as arteria buccinatoria in the 60 mm embryo from the same vessel but somewhat more caudal. In the two last mentioned cases the ramus orbitalis is thus lacking. The arteria buccinatoria soon bends ventrorostrad running medially to musculus temporalis and the dorsal border of the lower jaw and penetrates between the masseter and buccinatorius muscles. On this part of its course it gives off branches to the temporal and masseter muscles. Anterior to the former it pierces the buccinatorius muscle and ramifies, sending small branches to this. For a considerable extent of its course arteria buccinatoria is accompanied by the buccinatorius nerve.

Of the anterior branches of the internal maxillary artery the greater palatinal and the sphenopalatinae take a slightly medial direction. The first mentioned branch soon sinks down into the palate and runs rostrad ventrolaterally to the ductus naso-pharyngeus. Further rostrad, where the partly formed palatum durum is constituted by the maxillary bone, the greater palatinal artery runs in the angle between the processus alveolaris and the processus palatinus of the maxilla, the foramen palatinum in the adult being situated on the sutura palato-maxillaris, where this laterorostrally bends sharply caudad. The most anterior part of arteria palatina major does not enter the nasal cavity through the foramen incisivum but furnishes the alveolus of the upper incisor. This we have established in the 60 and 80 mm embryos.

The sphenopalatinal artery originates from the same trunk as the greater palatinal and runs in its distal parts dorsally to this. It extends rostromediad and, passing ventrally to the ventral border of the nasal capsula, it bifurcates. Its medial branch, arteria nasalis posterior septi, follows the ventral border of the nasal septum rostrad and still further anterior laterally to the organ of Jacobson. The lateral branch, arteria nasalis posterior lateralis, enters the nasal capsula and follows the still blastematic ventral edge of the maxillo-

turbinal,[1] providing a small branch for the glandula nasalis lateralis in the recessus maxillaris.

On the lateral trunk of the internal maxillary artery the infraorbital artery is the medial branch. It gives off two twigs, the arteriae alveolares superiores anteriores already in the orbit, passes through the infraorbital canal into the face and runs along the upper lips giving off branches to muscles and the skin.

The ramus malaris is the lateral branch of the lateral truncus. It runs rostrolaterad through the orbit, gradually bending dorsad and caudad, and passing ventrally and rostrally to the periorbit. Taking this course it steals to the ventral surface of the musculus oculi obliquus inferior, to which it gives off a small twig. It then sends a short branch distally along the inferior canaliculus of the nasolacrimal duct, passes ventrally and rostrally to the ramification of this duct and gives off another branch, which in the same way follows the superior canaliculus, thus supplying the two palpebrae.

To the branches of the internal maxillary artery above described the small arteriae alveolares superiores posteriores must be added, originating in this embryo from the arteria maxillaris interna caudal to the two anterior bifurcations.

The scheme of the anterior ramification of arteria maxillaris interna is subject to individual variations. Despite this the malar artery and the infraorbital artery always have a common trunk.

II. The internal carotid near its origin gives off the occipital artery (*o.*) from its ventral wall, passes medially to the hyoid in cranial direction, approaching the anterior pole of the cochlear capsule. It enters into the cranial cavity between processus alaris and the cochlear capsule, thereby passing through the sinus cavernosus. During this part of their course the two internal carotids approach the median plane, to which they come nearest on a level with the hind part of the hypophysis, which they almost touch. Here, dorsally to the posterior border of processus alaris and still in the dura mater, the internal carotid branches into its caudal and cranial rami.

A. The rather small occipital artery (*o.*) bends laterally from its origin at the ventral wall of the internal carotid towards the rudiment of the tendon common to the digastric and stylohyoid muscles, passing rostrally to the glossopharyngeal nerve. On the right side it passes laterally, on the left side medially to vena jugularis interna, in both cases arriving at the posterior border of the paracondyloid process, around which it bends. To determine which of these two courses ought to be considered the normal one, we have examined the embryos of 36 mm and 42 mm body length. In the first case the occipital artery behaved on both sides as on the right side in the 33 mm embryo, in the second case the right and left sides coincided with the corresponding sides in

[1] The vessel pierces the blastema, on the lateral side of which it runs for some distance. In older stages it always runs medially to the maxillo-turbinal cartilage on the bottom of a small depression.



VOL
27
194

the 33 mm embryo. The medial course of the arteria occipitalis in relation to the internal jugular vein on the left side thus seems to be as "normal" as the lateral. When just passing the posterior border of the paracondyloid process the arteria occipitalis gives off the condyloid artery (*c.*) mediad. Proceeding along the lateral side of the caudal border of the paracondyloid process it branches off a dorsally directed ramus muscularis (*mu.*) and then runs caudad towards the foramen transversarium of the atlas, through which it passes. It cannot be traced any further in this embryo. In later stages (36, 42, 60, 80 mm body length) it gives off a small branch, which being the equivalent of the first ramus spinalis of the vertebral artery, enters the vertebral canal through the intervertebral foramen of atlas, in addition to several muscle branches. We have not been able to find any connection with the vertebral artery.

The condyloid artery extends mediad caudally to vena jugularis interna and passes through the hypoglossal foramen into the brain case, where it ramifies in the dura mater.

Ramus muscularis continues in the main direction of the occipital artery running ventrally to the lamina alaris, where it ramifies providing the numerous muscles inserted here.

B. Ramus caudalis (*ca.i.*), after entering the dura, for a certain distance runs medially to the trigeminal ganglion straight dorsad, then bends mediad at the caudal part of pedunculus cerebri and unites with its partner forming the basilar artery. Just at its bend anterior to the root of nervus oculomotorius the arteria communicans gives off the arteria cerebri posterior (*c.p.*), which immediately branches, and posterior to this nerve arteria cerebellaris anterior (*cb.a.*). The third ramus spinalis of arteria vertebralis passes into the vertebral canal between the axis and the third vertebra. They anastomose with the ventral spinal artery and join in the axis forming the basilar artery, which enters the brain case through the foramen magnum. A pair of posterior cerebellar arteries (*cb.p.*) originates from the basilar artery posterior to pons Varolii.

C. Ramus cranialis of the internal carotid extends rostrad dorsally to the optic tractus and joins its partner of the other side anterior to the optic chiasma forming the arteria cerebri anterior communis (*c.c.*), an arteria communicans anterior in the usual sense of the word being absent. It gives off three branches: the ophthalmic artery (*oph.*) on a level with foramen rotundum, the arteria cerebri media (*c.m.*) dorsal to foramen opticum and ramus ethmoidalis (*et.*) medial to the anterior root of ala orbitalis. The first mentioned ramification takes place in the dura mater, but the two vessels formed immediately pass within this membrane.

The large ophtalmic artery leaves the internal carotid mediorostrad, bends around the posterior root of ala orbitalis and leaves the brain case through the optic foramen. By this it passes ventrally to the optic nerve and gives off a number of small branches to the dura mater situated ventrally to this nerve.

In this embryo as well as in a specimen of 36 mm body length the ophthalmic artery on the right side branches already within the brain chase while on the left side not until it reaches the orbit. It provides the eyeball and all the extrinsic eye muscles with the exception of the inferior oblique muscle.

Arteria cerebri media, being the largest branch of the ramus cranialis of the internal carotid, sets off from the latter rostrolaterad and follows the sylvian fissure. Anterior to the branching off of this artery ramus cranialis (arteria cerebri anterior, *c.a.*) gradually bends towards the median plane to form the arteria cerebri anterior communis.

The ramus ethmoidalis bends rostrally and approaches the median plane only after having entered the area of the lamina cribrosa. It penetrates into the dura mater at a very acute angle and joins it partner of the other side forming in the centre of the fenestra olfactoria a short arteria ethmoidalis communis (*et.c.*). From this several small branches originate, which form a sub-dural rete ethmoidalis in the future bottom of the fossa ethmoidalis. This rete sends small arteries with the olfactory nerve fibres into the posterior part of the nasal cavity and into the dura mater. It has no connections with the vessels of the orbit. An arteria ethmoidea externa is thus missing. The rami ethmoidales of the two sides separate again anterior to the short common truncus and proceed laterorostrad towards the anterior part of the most rostral foramen cribrosum, which will later form the foramen cribro-ethmoidale. This portion of ramus ethmoidalis is on both sides doubled in this embryo with anastomoses between the two components. However, this arrangement seems to be rather variable. In the embryo of 36 mm body length this vessel is a single one, but a 42 mm embryo again shows it doubled. Near the most rostral foramen cribrosum the left ramus ethmoidalis gives off an arteria bulbi olfactorii anterior (*o.a.*), which enters the dura mater and gives rise to two branches, one for the rostral end of the olfactory bulb and one for the rostral end of the frontal lobe. On the right side this vessel originates from the anterior end of the arteria bulbi olfactorii medialis (cf. below). This section of ramus ethmoidalis which in relation to the conditions in earlier stages has been extremely lengthened, runs in the dura mater near the dorsal edge of septum nasi. In the 42 mm embryo the four vessels are squeezed out in one row between the basal parts of the hemispheres. Ramus ethmoidalis enters into the future foramen cribroethmoidale, where it ramifies into a medial and a lateral branch. The medial one enters with medio-rostral direction a narrow canal in the cartilage and appears on the surface of the nasal tectum in a small depression anterior to the small spina mesethmoidalis. It joins its partner of the other side forming an unpaired vessel, arteria medialis nasi (*md.n.*), which extends rostrad outside the nasal capsule. In the 60 mm embryo this vessel runs ventrally to the suture of the nasal bones. The lateral branch of ramus ethmoidalis which we shall call arteria ethmoidalis (*e.*) directly after its entry into the



VOL
27
194

nasal cavity gives off a ramus septalis (*se.*) which follows the line of fusion between the nasal septum and tectum while the main stem passes to the foramen epiphaniale and thence rostrad.

In this specimen we find remainders of the arteria bulbi olfactorii medialis (*o.m.*). On the left side it originates from the arteria cerebri anterior and extends rostrad within the dura dorsally to ramus ethmoidalis. About half way between its origin and the arteria ethmoidalis communis it gives off a laterally directed artery to the ventral and lateral surface of the hemisphere and simultaneously enters the dura. The corresponding vessel on the right side originates from the ramus ethmoidalis, as the proximal part of arteria lobi olfactorii medialis is lacking here. On the right side the ramus ethmoidalis simultaneously gives off a vessel, which bends rostrad and proceeds in this direction in the dura constituting an anterior portion of arteria bulbi olfactorii medialis. On the right side this artery near the arteria ethmoidalis communis gives off a dorsally directed branch, which runs within the dura along the medial surface of the hemisphere, whilst on the left side the arteria bulbi olfactorii medialis extends within the dura to the anterior end of bulbus olfactorius, where it joins the arteria bulbi olfactorii anterior.—In the embryo of 36 mm the arteria bulbi olfactorii medialis is totally lacking on both sides.

OL.
27
946

### 80 mm embryo, head length 18.5 mm.

The arteries differ from those of the preceding stage in the following respects.

Arteria thyreo-laryngea originates here from the ventral and not from the medial wall of the common carotid. The branching off of the lingual artery has been still more caudally displaced, so that it originates here from the common carotid and not as earlier from arteria carotis externa. Ramus externus of the external carotid, which extends dorsad caudally to the external meatus auditivus, ramifies in a somewhat different way. After a rather short course it gives off the external maxillary artery, proceeds further dorsad and branches in the superficial temporal artery and the great auricular artery. Arteria occipitalis originates from the dorsal wall on the left side of the external on the right side of the internal carotid. The branching off of this artery has also been displaced caudally in relation to the point of ramification of the common carotid. It runs dorsad medially to the digastric muscle together with the glossopharyngeal nerve, around which it winds nearly three quarters of a turn. The occipital artery, after having passed through the foramen transversarium of the atlas, provides several neighbouring muscles and gives off a small branch, which enters through the foramen intervertebrale of this vertebra. We have not been able to trace any connection between the occipital and vertebral arteries.

## Previous observations on adult animals.

The organs of circulation of the adult Procavia capensis have been briefly described in three specimens by GEORGE (1874). To this BEDDARD (1904, 1909) has added some notes on the arteries of the brain founded on a more extensive material. GEORGE's account is also especially detailed concerning the arteries of the brain. According to him the common carotid "... se termine par trois branches: l'artère occipital, la carotide interne, et la carotide externe (p. 49)". Our 80 mm embryo also shows the occipital artery as a branch of the internal or external carotids. As our series of older embryos certainly demonstrated a caudad displacement of the origin of the occipital artery in relation to the point of ramification of the common carotid, this discrepancy may be explained by the assumption that this process has still not finished in the 80 mm embryo, or does not proceed equally far as a consequence of individual variation. About the connection of arteria occipitalis with arteria vertebralis GEORGE writes: "... puis elle (the arteria occipitalis) transverse le trou de l'atlas, fournit plusieurs branches musculaires à la région occipitale, et se termine par l'artère cérébro-spinale, qui concourt à former le tronc basilaire, en s'anastomosant avec l'artère vertébrale.", and—dealing with the skeleton—the foramen intervertebrale of the atlas "... donne passage à l'artère cérébro-spinale (formée par la réunion de l'artère vertébral et de l'artère occipitale) ...". In no case have we been able to reveal any connection between the occipital and vertebral arteries. Unfortunately GEORGE does not give any information about the entrance of the vertebral artery into the vertebral canal. As far as we have been able to establish, the very small branch entering the foramen intervertebrale of the atlas, ramifies in the dura mater without attaining connection with the arteria vertebralis. The considerable length of the basilar artery is pointed out by BEDDARD (1904).

GEORGE describes the external carotid with its branches in the following way: "L'artère carotide externe, au niveau du condyle de la mâchoire, se divise en deux branches: l'artère temporale superficielle, et la maxillaire interne. Avant cette division, elle fournit une artère très-importante, la linguale, et plusieurs rameaux secondaires qui se distribuent au pharynx, aux joues et aux lèvres." We have not been able to find in any of our specimens an arteria temporalis superficialis originating from the external carotid of the place mentioned. Again it may be a case of variation, the specimen of GEORGE being provided with a rarely occurring vessel. The arteria temporalis superficialis described by him furnishes the muscles and the skin of the face, of the zygomatic and anterior regions of the ear. This roughly coincides with the distribution of ramus externus of carotis externa with its branches, about which GEORGE does not speak at all. It may be that ramus externus in his specimen



VOL
27
194

originates from the external carotid much more distally than usual. He proceeds:

"La maxillaire interne fournit de nombreuses branches (dentaire inférieure et supérieure, ptérygoïdienne, temporale profonde, buccale et palatine). Mais la plus intéressante de toutes est l'artère ophtalmique, qui entre dans le crâne par le tron orbitaire, pour se distribuer à toutes les parties constituantes et accessoires de l'oeil." Here again there exist great discrepances between GEORGE's description and our observations. A branch of the internal maxillary artery, the ramus malaris, furnishes one of the extrinsic eye muscles and some structures in the palpebrae, whilst the eyeball and the remaining extrinsic eye muscles are provided by the ophthalmic artery, a branch of the internal carotid.

GEORGE remarks that the internal carotid does not show any retia mirabila, as found in the pig, the ruminants, the cat, etc. Our account of the arteries of the brain may be completed by GEORGE's descriptions of their further courses:

"En arrière de la protuberance annulaire, on voit naître à droite et à gauche des rameaux assez volumineux, les artères cérébelleuses postérieures, qui fournissent des artérioles aux parties postérieures et latérales du cervelet. Au niveau de la protubérance, plusieurs paires de ramuscules nés du tronc basilaire se distribuent à la protubérance annulaire. Au commencement des pédoncules cérébraux, le tronc basilaire se termine en se bifurquant pour fournir les artères communicantes postérieures qui vont se jeter dans le carotide interne."

"Les artères cérebelleuses antérieures se dirigent en dehors et en arrière, en contournant les pédoncules cérébraux, et se distribuent à la partie antérieure du cervelet. Les artère cérébrales postérieures se bifurquent presque aussitôt après leur origine; la branche antérieure gagne la fente de Bichet et se distribue à l'intérieur de l'hémisphère; la branche postérieure contourne l'extrémité postérieure du cerveau, et lui fournit de nombreuses branches qui se dirigent à sa surface d'arrière en avant, et s'anastomosent à leur terminaison avec les artères cérébrales moyennes."

"L'artère cérébrale antérieure s'engage immédiatement entre la commissure des nerfs optiques et le lobe olfactif, qu'elle contourne; elle monte ensuite le long de la face interne de l'hémisphère, se dirige en avant, et contourne l'extrémité entérieure du corps calleux; puis elle se dirige en arrière en fournissant plusieurs branches ascendants, et s'arrête vers l'extrémité postérieure du corps calleux. Ses branches terminales s'anastomosent avec celles de l'artère cérébrale postérieure. L'artère cérébrale moyenne contourne la saillie du lobule mastoïde, se loge dans la dépression qui représente la scissure de Sylvius, et se divise, après un court trajet, en deux branches, l'une antérieure, l'autre postérieure, qui se subdivisent à leur tour et s'anastomosent par leur branches terminales avec les artères cérébrales postérieure et antérieure."

## DISCUSSION.

### Aortic arches.

CONGDON (1922) drew attention to the unsatisfactory state of the terminology of the ventral connections between the heart and the branchial arterial arches. "Few authors are in complete agreement in the use of such fundamental terms as aortic trunk, bulb or ventral aorta." On reviewing the literature on the development of the aortic system in mammals we find the term "ventral aorta" used in rather different ways. TANDLER (1902) and STRUTHERS (1930) both mention an anterior and a posterior trunk of the ventral aorta. The first and second aortic arches originate from the anterior trunk, the third, fourth and pulmonary arches from the posterior trunk. Struthers, however, includes the lateral parts of the aortic sac in the "ventral aorta". LEWIS (1906), BREMER (1912) and REGAN (1912) use the term for the posterior trunk, whilst BREMER (1912) terms the ventral rostrocaudad-running portion of the first arch in this way. The aortic sac is called ventral aorta by HEUSER (1923) and this term is used by LLORCA for a certain part of the sac, a common trunk for the third and fourth arches. Finally O. HERTWIG (1915, p. 671) in his "Lehrbuch der Entwicklungsgeschichte des Menschen und der Wirbeltiere" uses truncus arteriosus and aorta ventralis synonymously. The same seems to be done by GOODRICH (1930, p. 524) in his "Structures and Development of Vertebrates" and in Anamnia the posterior pairs of afferent branchial vessels are often said to be given off from the truncus arteriosus.

LEWIS (1906) defines the aortic arches "... as vessels extending from the ventral aorta and formed either between the successive pharyngeal pouches, in front of the first, or behind the last." This definition does, however, not hold for the sixth chelonian arch, which was shown by SHANER (1921) to lie lateral to the postbranchial body. In consequence of this we have to define the ventral aorta as a paired or unpaired vessel chiefly extending rostrocaudad and connecting the ventral roots of the aortic arches with one another and with the truncus arteriosus, which consequently does not give off aortic arches. In this sense the term "ventral aorta" has been used by KERR (1919) and DALCQ and GERARD (1935) in their textbooks of embryology. Instead of this the caudally directed common trunk giving off the fourth, fifth and sixth aortic arches is frequently considered in mammalian as well as in reptilian embryology to consist of a sequence of segments belonging to the enumerated arches. On the other hand, most schemes in earlier text books of human anatomy show the aortic arches arising from a pair of longitudinal ventral aortae. CONGDON (1922), dealing with human embryology and introducing the term aortic sac, disagrees with this: "There are at different times a few temporary channels leading from



VOL. 27 1946

the sac which by their approximately cranio-caudal course, resemble fragments of ventral aortae. Such are the longitudinal segments that appear in the late history of the first and second arches and the paired sprouts, which give rise to the proximal parts of the pulmonary arches and the primitive pulmonary arteries. These vessels are truly indicative of a general structural plan, which in some lower vertebrates is elaborated to a degree that permits the development of paired ventral aortae. There is no phase of human development, however, in which such vessels exist."

The factor complicating these questions is the formation of the aortic sac, in which process the ventral aortae seem to be involved. However, as far as we have been able to ascertain, this process has not been thoroughly analyzed.

A very detailed account of the developmental history of the aortic system in the rat is given by TANDLER (1902). The paired state of the posterior ventral aortae appears in a stage with the three first aortic arches (fig. 3, p. 299), so that the third arch does not originate from an aortic sac, but from the ventral aorta. At a later stage (fig. 8, p. 302), where all the aortic arches are formed, the posterior border of the aortic sac has been displaced caudad, but only just far enough to permit the third arch to originate from the aortic sac. Thus there are still two rather long posterior ventral aortae from which the fourth and sixth arches originate. The displacement caudad of the posterior border of the aortic sac involves the fusion of the posterior ventral aortae and this process can be followed step by step in TANDLER's account. This process proceeds up to a point near the origin of the pulmonary arches before the separation of the pulmonary trunk from the aortic trunk takes place.

According to STRUTHERS' (1930) account of the development of the aortic system in the porcupine (Erethizon dorsatus) there are typical anterior and posterior ventral aortae in stages of this animal with two and four completed aortic arches. In early stages there is thus good agreement with the rat.

In Mus and Erethizon the fusion of the posterior ventral aortae is greatly delayed in relation to their formation. This is, however, not the case in all mammals. BREMER (1912), studying the development of the primary arterial system in Lepus, describes plexiform ventral aortae in early stages. "While the second arch is becoming established the plexus of the ventral aorta is extending still further caudad, and again giving off lateral branches, which run between the entodermal pouches to the dorsal side of the pharynx, and again are met by shorter growths from the dorsal aorta." In this stage (BREMER's fig. 8, p. 124) "the plexus of the ventral aortae" has to a great extent lost its paired character, anastomosis between the aortae of the two opposite sides being formed as precursors of the total fusion of these paired structures. Thus the posterior ventral aortae between the second and fourth aortic arches here already fuse before they are fully developed. In a later stage (BREMER's fig. 9, p. 125), in which the fourth arch originates from the aortic sac, we meet again

plexiform paired posterior ventral aortae extending caudad as a network representing the pulmonary arteries. In this region the fusion of the ventral aortae takes place rather slowly as in other mammals. LEHMANN's (1905) more superficial description of Lepus does not permit to draw any conclusions in this matter. Her figures, however, may well be interpreted in the same manner.

A very interesting series of the aortic arches in the cat at different stages has been described by COULTER (1909). Here also the posterior ventral aortae are of short duration. In a stage with the three first arches a paired ventral aorta exists between the second and third (COULTER's fig. 2, p. 580), but these have already fused before the fourth arch has been completed (COULTER's fig. 3, p. 581). When this is the case the ventral aortae between the fourth and the third arches already fuse before the continuations of the ventral aortae have grown out very far (cf. the cat embryos described by HUNTINGTON 1919).

Although a great many investigations (LEHMANN 1905, REGAN 1912, HOFMANN 1914, SABIN 1917, HEUSER 1923, CONGDON and WANG 1926, LLORCA 1933) have dealt with the aortic arches in the pig it is rather difficult to gain sufficient information regarding the formation of the posterior ventral aortae and their fusion. From HEUSER's figures 12 and 20 it may be seen that the posterior ventral aortae already fuse between the second and third arches before they have extended behind the third arch, while they have fused between the fourth and fifth arches before extending behind the pulmonary arches (HEUSLER fig. 21, plate 3). This places the pig in a group together with the rabbit and cat, which view is also supported by LEHMANN's figures. There is no doubt that man also belongs to this group (cf. CONGDON 1922, figs. 31—32 and figs. 33—34). Thus the posterior ventral aortae fuse in their anterior portion very soon after formation, thus losing their paired character. This is, however, no reason to deny their morphological significanse.

Summing up, we arrive at the following conclusions:

1. The aortic sac is to a great extent formed by fusion of the posterior ventral aortae and must consequently be considered as a specialized part of these (cf. definition above).

2. This fusion takes place in some mammals immediately after the formation of these vessels, but in others it is delayed, so that the paired state persists until a later stage.

In most Sauropsida paired anterior and posterior ventral aortae are met with during the development of the aortic system. This is shown in Chelonia (SHANER 1921), Rhyncocephalia (WYETH 1923), Crocodilia (HOCHSTETTER 1916), Aves (KASTSCHENKO 1887), but seems to be less obvious in Lacertilia (cf. PETES 1901, GREIL 1903). Consequently we are inclined to consider those Mammals, (Mus, Erethizon) in which the posterior ventral aortae fuse late to be more primitive than those (Lepus, Felis, Sus, Homo), in which these vessels

fuse early.[1] It is difficult to place Procavia in either of these two groups because of the complicated mode of development of the most posterior arches. If one only considers the posterior ventral aortae, which do not appear paired for long during the development, Procavia must be referred to the less primitive type. On the other hand, the occurrence and transformations of the provisional arches seem to reflect ancient phylogenetic events.

The numbering of the provisional arches is of importance for the following discussion. The question is: Does the provisional fifth arch represent a reptilian fifth arch or does it, in conformity to its future destiny, constitute a reptilian fourth arch? In case of the second alternative the provisional fourth arch must be considered as an accidental structure. Evidence to the contrary is its occurrence in two successive stages (the 4.5 and 5.5 mm embryos). Further the provisional fifth arch takes the same position in relation to the caudal pharyngeal complex as in Chelonia (cf. SHANER 1921) the fifth aortic arch in relation to the fifth pharyngeal pouch, i.e. lateral to the most anterior part of the pouch. The caudally directed trunk extending from the provisional fifth arch in the 4.5 mm embryo must be considered as the dorsal root of a provisional sixth arch, the connection of which with the dorsal aorta will be discussed below (p. 136). As in reptiles this provisional sixth arch has a dorsal trunk running into the dorsal aorta in common with the fifth arch. The dorsal root of the provisional sixth arch has developed before the appearance in the corresponding ventral region of a caudal ventral aorta and extends lateral to the caudal portion of the caudal pharyngeal pouch as does the sixth arch in Chelonia and some other reptiles (SHANER 1921). Then the provisional sixth arch becomes reduced, either totally, the small protrusion occupying its place in the 5.5 mm embryo being formed a new, or partially, the protrusion in question being its remnant. This grows out to the dorsal part of the pulmonary arch, which lies here (6 mm embryo), as in other mammals, medial to the ultimobranchial body, being, as stated by SHANER, morphologically another vessel than the sixth aortic arch in turtles. The origin of the pulmonary arch from the provisional fifth arch is manifested in later stages (up to the 10 mm embryo) with the two mentioned arches opening together into the dorsal aorta.

According to the above comparisons the following interpretation of the developing aortic arches in Procavia seems possible. The provisional fourth arch seems to correspond to the fourth aortic arch of reptiles. As it is a regressive structure disappearing already during early ontogeny it has to a great extent been incorporated in the fifth aortic arch, which in its dorsal portion is re-

[1] An interesting variation in the relations between the original distal end of the truncus arteriosus and the future aortic arches in the Amniota may be pointed out. This early end of the truncus is situated at the second arch in Mammals (TANDLER 1902, COULTER 1909, BREMER 1912, CONGDON 1922, DAVIS 1923, HEUSER 1923 and others) and Rhyncocephalia (WYETH 1924) whereas it is to be found at the third arch in Chelonia (SHANER 1921) and Aves (SABIN 1917, HUGHES 1934).

presented by the provisional fifth arch. The definite fourth arch would thus correspond to the fifth arch in reptiles. The provisional sixth arch, corresponding to the dorsal rudiment of the sixth in reptiles, soon disappears yielding its place to the mammalian pulmonary arch, which is a neomorph.

It follows from this interpretation of the developing aortic arches that the reduction in number of the reptilian pharyngeal pouches has affected the fourth one. MINOT (1918) states that some authorities consider a pouch between the present third and fourth in mammals having been lost. KINGSBURY (1915), however, knows of no clear evidence to support this.

We shall now try to find structures in other mammals which may support our interpretations for Procavia and make a generalization of these possible. To facilitate the survey of the literature we have compiled some facts in a table (p. 137). This is, however, by no means complete, but is meant to show the actual variation of some structures.

The fourth aortic arch in Procavia was identified with the fifth arch in reptiles mainly because of the existence of the provisional fourth arch. The existence of the remainder of such a reduced arch would become manifest either through the occurrence of an isle in the dorsal root of the fourth aortic arch just ventral to the dorsal aorta or in a striking breadth of the connection of this arch with the dorsal aorta. As we have seen in Procavia the reduction of the provisional fourth arch is also accompanied by the formation of an isle. Consequently the appearance of more than one isle may be expected. Before entering into the discussion of the table, we have to point out some facts concerning the formation of aortic arches. In rabbits LEWIS (1904) showed the first arch to arise from an angioblastic net together with the ventral and dorsal aortae, and BREMER (1912) found the second, third and fourth arches to be preceded by a vascular plexus from the ventral aorta. BREMER describes this to be potentially double for the second arch and multiple for the succeeding ones. According to CONGDON (1922) in human embryos simple loops not infrequently become detached from the aorta at the upper end of the visceral arch before any definite sprout has become establised. They may remain for a time as a part of a complete vessel enclosing isles, which as pointed out by LEWIS (1906) are of general occurrence in mammals. After this account it seems very difficult to demonstrate a more frequent occurrence of isles in the dorsal root of the fourth arch than in that of preceding arches. This all the more as the descriptions are often not sufficiently detailed, the available cases being limited to those which are illustrated. Older stages with the anterior arches in regression or reduced are much more frequently portrayed than younger ones, this making any kind of statistics impossible. Our general impression is, however, that isles in the dorsal roots in well-developed first, second and third arches are much less frequent than in that of the fourth arch. On the other hand isles are sometimes found in the independent dorsal root of the pul-



VOL
27
194

monary arch occuring in most mammals (cf. LEWIS 1906, COULTER 1909). As seen from table 1 the occurence of isles in the dorsal root of the fourth aortic arch sems to be restricted to Erethizon, Mus, Sus and Homo. In Sus and Homo we also find this root to be very broad in some cases but without isles. Apart from Erethizon, of which only one embryo of suitable age is available, the frequency of these forms of the fourth arch is rather high, being about 50 % in Mus and Sus and 100 % in Homo. Not even in the fourth arch do isles generally occur in all mammals. This may somewhat strengthen the importance of the result shown in the table.

Another typical arrangement in Procavia is the common dorsal root of the fourth and the pulmonary arches. Table 1 shows that this is the case not only in Procavia, but also in man. In man, the two arches originate in young stages (4.9—5 mm) from a short common dorsal trunk, which, contrary to what happens in Procavia, soon disappears, so that the two arches in 7 mm embryos open into the dorsal aorta separately but very close together. We shall return later to the single pig embryo which is characterized by having the two relevant arches joined in a common dorsal trunk. In all other mammals represented in table 1 the dorsal roots of the fourth and aortic arches are well apart from their first appearance.

A very interesting structure is described by TANDLER (1902) in a 3 mm rat embryo. The first to third aortic arches are developed in the usual way and will not be further discussed. Posterior to the third arch a large caudad-running trunk represents, according to TANDLER, the caudal portion of the ventral aorta. It bends dorsad under the third pouch and joins the dorsal aorta. The dorsad extending portion of the vessel, being very broad and enclosing two isles, is interpreted as a fourth arch. From the bend a thin branch is given off running caudad. This branch "biegt kurz danach dorsalwärts ab, umgreift die früher als vierte Schlundspalte beschriebene Ausbuchtung des Pharynx an der lateralen Seite und löst sich hier in einzelne Bluträume auf, die sich bis in ein aus der Aorta dorsalis stammendes dorsales Anfangsstück verfolgen lassen. Dieses Gefäss ist der sechste Aortenbogen, der sich also in diesem Stadium eben entwickelt." It is obvious that this branch running laterally to the caudal pharyngal complex cannot represent a pulmonary arch, and as it thus disappears later the description seems to indicate an incipient reduction. It shows great conformity, both in its position and in its later history, to the structure which in the 5.5 mm embryo of Procavia connects the provisional sixth arch with the dorsal aorta. The conformity of the aortic arches in this embryo with those in TANDLER's is also in other respects so striking, that an interpretation of the different parts in agreement with our ideas gained from Procavia is very tempting. The broad portion interpreted by TANDLER as a fourth arch would correspond to a fourth and a fifth arch and the trunk interpreted by TANDLER as a caudal ventral aorta would really represent this structure only in its anterior

portion and in its posterior portion a trunk common to the fourth and fifth arches. TANDLER's "sixth arch" would thus join the fifth arch at some distance from the dorsal aorta. Irrespective of whether this interpretation is right or otherwise, the connection in question in Procavia and Mus can neither correspond to the sixth arch in reptiles nor to the pulmonary arch in mammals. As it appears comparatively early in the ontogeny, that is before the pulmonary arch, it is probably a phylogenetically old structure arising before or together with the deplacement of the reptilian sixth arch by the mammalian pulmonary arch. We shall therefore term it the prepulmonary arch. In Procavia it disappears totally, whereas in Mus its most dorsal portion is in all probability involved in the formation of the pulmonary arch. The dorsal root of the pulmonary arch in Procavia and Homo does thus not seem to be homologuous with that in other mammals.

The dorsal roots of the fourth and pulmonary arches, although being well apart in some mammals, may, however, be connected with each other, which occurs especially frequently in the pig (cf. table 1). The connection mostly consists in a short trunk situated near the dorsal aorta and parallel to this. In one case the enclosed foramen is divided in two by a short anastomosis between the inter-arch connection and the dorsal aorta (the upper 8.6 mm pig embryo in table 1). In other cases the foramen seems to have been closed, a connection appearing only in the extraordinary breadth of the dorsal aorta between the two arches. When such cases are also counted, we find the connection between the dorsal roots of the fourth and pulmonary arches in 70 % of the pig embryos.[1] Both in the pig and in the rat this inter-arch connection appears rather late in the development. In the pig its formation is probably associated with the gradually occurring approach of the roots of the fourth and pulmonary arches, which can easily be followed in HEUSER's (1922) figures. With respect to its position it corresponds only in part to the prepulmonary arch; its rather late appearance also speaks against a homology with this structure. The abnormal mode of development of the dorsal root of the pulmonary arch in the 5.5 mm pig embryo in table 1 shows that the dorsal "inter-arch" connection may, under certain conditions, also appear earlier. Here the normal dorsal root of the pulmonary arch is lacking, the connection of the pulmonary arch with the dorsal aorta being accomplished only by the "inter-arch" connection and the dorsal root of the fourth aortic arch.

As to the so-called "fifth arch", the existence of which has often been doubted, our interpretation of the findings in Procavia excludes the existence of this structure. We have thus little reason to review the vast literature on this subject but may refer to the account recently given by HAMMOND (1937)

[1] A less completely developed connection of this kind is found in four pig embryos of 8.5—10 mm length illustrated by REGAN (1912). This extends dorsocaudad from the dorsal root of the fourth arch to the dorsal aorta (cf. also LEWIS 1906, fig. 28).

TABLE 1.

| | Stage mm | Author | Dorsal root of fourth arch contains one or more iles | Dorsal root of fourth and pulmonary arches common | Dorsal root of fourth and pulmonary arches well apart | |
|---|---|---|---|---|---|---|
| | | | | | Without connection | Connected by a dorsal anastomosis |
| Talpa | 4.5 | SICHER 1912 | — | — | + | — |
| | 5 | SOULIÉ-BONNE 1908 | — | — | + | — |
| Lepus[1] | 4.4 | LEWIS 1906 | — | | | |
| | 5 | „ 1906 | — | — | + | — |
| | 7 | „ 1906 | — | — | + | — |
| Erethizon | 6.5 | STRUTHERS 1930 | + | — | — | +[2] |
| Mus | 3 | TANDLER 1902 | + | — | —[3] | — |
| | 3.5 | „ 1902 | — | — | + | — |
| | 3.5 | „ 1902 | + | — | + | — |
| | 4 | „ 1902 | + | — | + | — |
| | 5.5—6 | „ 1902 | — | — | — | +[4] |
| | 6.5 | „ 1902 | — | — | — | + |
| Felis | 4 | HUNTINGTON 1919 | — | — | + | — |
| | 5 | COULTER 1909 | — | — | + | — |
| | 5 | „ 1909 | — | — | — | + |
| | 5.6 | „ 1909 | — | — | + | — |
| | 6 | HUNTINGTON 1919 | — | — | + | — |
| | 7 | COULTER 1909 | — | — | + | — |
| | 9 | „ 1909 | — | — | + | — |
| Sus[5] | 5.5 | LEWIS 1906 | — | + | — | — |
| | 6 | HEUSER 1922 | + | — | + | — |
| | 6 | LLORCA 1923 | — | — | + | — |
| | 6.5 | „ 1923 | —[6] | — | — | + |
| | 8.2 | HOFMANN 1914 | + | — | + | — |
| | 8.5 | REGAN 1912 | + | — | — | + |
| | 8.6 | „ 1912 | — | — | — | + |
| | 8.6 | „ 1912 | — | — | — | + |
| | 9 | LEWIS 1906 | — | — | — | + |
| | 9 | „ 1906 | + | — | — | + |
| | 9.5 | LLORCA 1923 | — | — | — | + |
| Bos | 6.5 | GOLUB 1931 | — | —[7] | | |
| | 7.75 | „ 1931 | — | —[8] | — | + |
| | 8 | HAMMOND 1937 | — | — | + | — |
| Tarsius | 4.7 | HAFFERL 1919 | — | | | |
| | 6.7 | „ 1919 | — | — | + | — |
| Homo | 4.9 | INGALLS 1907 | + | + | | |
| | 5 | TANDLER 1902 | + | + | | |
| | 5 | CONGDON 1922 | +[9] | + | | |
| | 7 | ELZE 1907 | —[6] | —[7] | | |
| | 7 | GOLUB 1931 | + | —[7] | | |

[1] According to LEHMANN (1905) embryos of 11, 11 1/2 and 12 days correspond to those in the table. [2] Connection confluent with the dorsal aorta. [3] Not homologous with the pulmonary arch. [4] Connection situated far ventrally. [5] 5 embryos 20 to 21 days old illustrated by LEHMANN (1905) show the same features. [6] Dorsal root very broad. [7] The two arches join the dorsal aorta close together. [8] Information lacking. [9] Right side. The left dorsal root very broad.

regarding the present state of the problem. However, our interpretation makes a new element available in the discussion, namely the reptilian sixth arch. This structure appears in reptiles after the fifth arch and takes its origin from this arch both dorsally and ventrally. In reptiles it lies lateral to the ultimobranchial body which in mammals is now generally considered "to be a prolongation of the pouch-forming area of the pharynx, out of which a fifth pouch occasionally develops as a lateral outgrowth, just as in the turtle" (SHANER 1921). As the reptilian fifth arch may possibly be supposed to have been involved in the formation of the aortic sac the reptilian sixth arch might be expected to originate from this in mammals. We may perhaps even count with a delayed appearance of a prepulmonary arch, which is partly lateral to the caudal pharyngeal complex. The combination of these two structures in different ways already implies some different possible arrangements of a "fifth arch". It may have a dorsal root in common with the fourth or the pulmonary arch and a ventral root originating from the fourth arch or the aortic sac, but must extend laterally to the ultimobranchial body. "Fifth arches" fullfilling these conditions have been described, e.g. in Talpa (SOULIÉ and BONNE 1908), Homo (TANDLER 1909), Sus (REGAN 1912) and Tarsius (HAFFEL 1919). To this we must add the tendency to form irregular sprouts in the region between the fourth and pulmonary arches as pointed out by LEWIS (1906), REGAN (1912) and HEUSER (1923).

In regard to general developmental changes in the aortic arches, the caudal shifting of the blood stream from heart to dorsal aorta, the disintegration of the arch system and its displacement in connection with the descending of the heart in the thorax, Procavia resembles other mammals.

## Basilar artery.

Since HIS' (1880) account of the formation of the basilar artery this has been known to arise by the fusion of two vessels extending longitudinally along the ventral surface of the cephalic portion of the nerve tube. HIS, however, erroneously termed these vertebral arteries, which name was long established in the literature. The mistake was revealed by MACALISTER (1886), who found these vessels to correspond with those running along the ventral surface of the spinal cord; this was confirmed by DE VRIESE (1905) in the rabbit. The name longitudinal neural arteries was introduced by SABIN (1917) in her study of chick embryos.

As in the earliest stage of our Procavia the longitudinal neural arteries have already been formed, we are not able to contribute to the early history of these vessels. According to SABIN they arise by the junction of a prolongation of the ramus caudalis of the internal carotid with a cranial extension of an anastomosis of segmental arteries. It is possible that a portion situated anterior to the seg-



VOL
27
194

mental arteries may also be formed by anastomosis, since DE VRIESE illustrates in rabbit embryos of 4 to 5 mm some very fine connections between the anterior part of the longitudinal neural arteries and the internal carotid, these vestigeal connections being possibly homodynamous with segmental arteries. Such presegmental branches of the dorsal aorta have also been described in Mus (TANDLER 1902) and Homo (cf. EVANS 1911). CONGDON (1922) concludes from the observations of other authors that in man "all the cranial members of the segmental series, as far back as the first cervical, contribute by anastomosis to the formation of the longitudinal neural arteries". Contrary to this, the neurals in our earliest stage of Procavia join only the third and following intersegmental arteries, the more anterior members of this series seeming to be missing. This probably means that the anterior intersegmental arteries disappear earlier than in the other mammals studied in this respect (Mus, TANDLER 1912; Erethizon, STRUTHERS 1930; Homo, cf. EVANS 1911).

In early stages of Procavia the longitudinal neurals have very delicate walls and are of a somewhat irregular shape, giving off numerous side branches as in man (CONGDON 1922). This is the first generation of neurals, characterized by their very intimate contact with the brain surface. As far as we have been able to find, there are no statements regarding this relationship in the literature. The figures given by DE VRIESE of a 6 mm rabbit embryo show the neurals situated at some distance from the surface of the brain. The formation of the second generation, the secondary longitudinal neurals, has already started in the occipital and cervical regions in our earliest stage. Ventrally directed protrusions occur here, extending in their end parts rostrocaudad. They join together forming a new trunk, which is situated lateroventral to the primary neural and connected with this by numerous anastomoses. As this process proceeds rostrad, the secondary longitudinal neural arteries become stronger than the primary ones, which by degrees begin to break into short segments and disintegrate. In the 7.5 mm embryo only very small remnants of the primary neurals are left. The temporary duplication of the neurals is very clearly seen in the posterior portion of the vessels, being less obvious more anteriorly. In this kind of formation the secondary longitudinal neurals become distanced from the brain surface and embedded in mesenchyme.

Contemporanously with the replacement of the primary longitudinal neurals by the secondary ones the formation of the basilar artery takes place. This has already been initiated in our earliest stage, three connections between the neurals being present in the 4.0 mm embryo. The most posterior of these belongs to the second generation of neurals, the two anterior ones to the first generation.

The longitudinal neural arteries are generally described as approaching each other before the formation of the basilar artery. CONGDON (1922) has devoted himself to this question and performed exact measurements on a series of

stages in man. He finds that the interval between the axes of the vessels remains constant and only the adjacent walls of these approach owing to the increase in diameter of the vessels. Our reconstructions (figs. 1, 3 and 5), however, show that an important mutual approach of the longitudinal neural arteries occurs in Procavia. Simultanously with this the connections increase in number and width and those belonging to the primary neurals are replaced by others belonging to the secondary ones.

DE VRIESE (1905) states that the neurals during the formation of the basilar artery, after having formed strong transverse anastomoses, partly disappear, the right or the left segment between two anastomoses being reduced. The same is found by CONGDON (1922) to occur in man. LEHMANN (1900), however, is of the opinion that fusion is more frequent in the formation of straight than of tortuous basilar arteries. That this process also plays a certain rôle in Procavia is learned from the 7.5 mm embryo, in which a segment of the left longitudinal neural is missing and another seems to be disappearing. This process seems, however, to be of less importance in man, probably owing to the vessels being able to fuse more completely because of their mutual appraoch.

VOL
27
194

## Origin of the external carotid and the development of the stapedial artery.

Soon after the third aortic arch has obtained its full size the ventral portions of the first and second aortic arches have disappeared. Their remnants probably form a part of the extensively ramifying system of lacunae which pierces the ventral portions of the mandibular and hyoid arches. In the 5.5 mm embryo the first and second arches are connected ventrally to the pharynx by a slightly branching lacuna which in its longitudinally extended portion probably corresponds to the longitudinal portion of the first aortic arch in the 4.0 mm embryo. It must be noted that a branch of this lacuna extends along the mandibular division of the trigeminal nerve on the lateral side of the latter, constituting the early rudiment of arteria alveolaris inferior primaria (terminology according to TANDLER). The lacuna has no connection with the aortic sac. The anterior border of this shows no protrusions that might possibly be interpreted as sprouts of an external carotid. When this appears in the 7.5 mm embryo it must consequently be a new vessel. In this respect Procavia coincides with Homo, in which, however, the external carotid appears as a rudiment near the median plane and is then gradually withdrawn from the midline (CONGDON 1922). After this displacement it is given off from the third arch, near the junction of this with the aortic sac as in Procavia. In other mammals (Erethizon, Mus, Sus, Bos, Tarsius) the external carotid is considered to develop from the ventral remnants of the first and second arches. This difference seems, however, to be of less importance, as the new branches constituting the external

carotid according to CONGDON (1922), probably link up with endothelial channels left by the regression of the first and second arches.

The external carotid joins the lacuna on the lateral side of the trigeminal mandibular division. At their appearance the dorsal roots of the first and second arches are very small, almost similar to capillaries. According to CONGDON (1922) they should be termed "later mandibular and hyoid arteries". The proximal portion of the latter is the equivalent of BROMAN's (1898) hyostapedial artery in man. Of the two distal branches of this the posterior one was called arteria hyoidea by GRADENIGO (1887) whereas the anterior one is the arteria stapedialis. The abnormal course of the stapedial artery in the 15.5 mm embryo probably depends upon the reduction of the dorsal instead of the ventral root of the second aortic arch. Another explanation would be that the hyoid artery has developed in conformity with the state described in Amia by ALLIS (1912), forming an arteria hyoides afferens secundaria. The hyostapedial artery, thus becoming less indispensable, would then have disappeared.

VOL. 27 1946

According to TANDLER (1902) the three branches of the stapedial artery, ramus superior, ramus inferior and ramus mandibularis belong to the first aortic arch and are only taken over secondarily by the arteria stapedialis. In Procavia some of these important branches already originate when first seen from the stapedial artery, the dorsal root of the first aortic arch only forming one single vessel (cf. the 9 mm embryo). This runs in its distal part together with the maxillary division of the trigeminal nerve, later providing the palate, the nose and the upper jaw, and it ought consequently be termed ramus infraorbitalis. The stapedial artery, being just on the point of joining this ramus, shows a proximal rod-like ramus superior and a distal ramus inferior growing out towards the dorsal end of the arteria alveolaris inferior primaria. These conditions in Procavia are very similar to those described by HAFFERL (1921) in the lacertilian Platydactylus, which is considered to be a primitive reptile (FÜRBRINGER 1900, TANDLER *et al.* 1907). Here the stapedial artery forms a ramus superior and a ramus inferior but no ramus infraorbitalis. The first aortic arch is represented by a nasopalatin or Vidian artery which runs close together with the Vidian nerve straigth laterad crossing the basipterygoid process on the lateral side of the latter. This implies that the vessel probably occurs on the morphological caudal side of the process since this is directed rostrolaterally in Geckonids as in most Lacertilian. The Vidian artery then gives off a branch laterad, which follows the maxillary division of the trigeminal nerve as arteria infraorbitalis, whereas the main trunk follows the Vidian nerve. As in Procavia the Vidian nerve follows the internal carotid cranially until this gives off the first aortic arch, together with which it leaves the carotid. Comparing the proximal portion of the Vidian artery in Platydactylus and that of the ramus infraorbitalis in Procavia we find some essential points of agreement. They constitute the dorsal root of the first aortic arch, and run straight laterad

passing caudally to the basipterygoid process, represented in Procavia by a very thin blastema of the processus alaris in the 11 mm stage. They differ, however, in their relation to the Vidian nerve. The Vidian artery runs close together with this nerve, whereas ramus infraorbitalis, after its straight lateral course, runs parallel to the Vidian nerve but at a considerable distance from it. The space between the vessel and the nerve is filled with mesenchyme, which we have studied especially in the very well preserved 11 mm embryo, where the remnant of the first aortic arch is still present. Anterior to this the ramus infraorbitalis passes rostrad medially to the mandibular division of nervus trigeminus. At this stage there is still no otic ganglion formed but in the following development (12 mm embryo) ganglion cells migrate to envelop this part of ramus infraorbitalis. Otherwise the mesenchyme develops into loose connective tissue. In view of the above, the homology between the proximal portion of the Vidian artery in Platydactylus and of the ramus infraorbitalis in Procavia is rather probable although not entirely proved. The portion of the ramus infraorbitalis anterior to its lateral bend (cf. fig. 6 *c*) would thus correspond to the ramus infraorbitalis in Platydactylus, which is also a lateral branch of the Vidian artery, whereas the distal portion of the Vidian artery would be missing in Procavia, its functions having been taken over by anterior branches of the ramus infraorbitalis.

VOL
27
194

In Erethizon STRUTHERS (1930) describes a Vidian artery springing from the internal carotid and joining the stapedial artery. It consequently corresponds to that portion of ramus infraorbitalis in Procavia running straight lateiad. Unfortunately its ontogenetic relations to the ramus infraorbitalis are not known. Another very interesting case similar to the conditions in Procavia was described as an abnormality by GROSSER (1901, fig. 9) in an embryo of Vespertilio murinus. On the left side of this embryo the infraorbital artery is given off by the internal carotid and corresponds to the dorsal root of the first aortic arch, whereas the ramus supraorbitalis and the ramus inferior take their origines from the stapedial artery.

In Procavia the three different rudiments of the stapedial system later join and the connections between the ramus infraorbitalis and the internal carotid and between the arteria alveolaris inferior secundaria and the external carotid disappear.

The occurence of a ramus superior is rather irregular in Procavia. In our younger stages it appears in the 9, 10, 12 and 17 mm embryos but is lacking in those of 11, 15.5 and 16 mm body length. It is a short dorsorostrally directed twig. In later stages the ramus superior develops to an arteria meningea media, the occurence of which is as irregular as that of ramus superior. This corresponds only to a ramus meningeus, a ramus supraorbitalis being totally absent.

In many mammals a ramus orbitalis connects the ramus infraorbitalis with ramus supraorbitalis stapediae. According to HOFMANN (1914) ramus orbitalis

in the pig runs along the lateral side of the maxillary division of nervus trigeminus craniad into the orbit where it joins the ramus superior and consequently is connected with ramus meningeus. In older stages of Procavia—19 mm and larger—we find an arteria meningea media anterior passing laterad to the maxillary division of nervus trigeminus through the foramen rotundum. This meningeal artery originates in two cases (19 and 60 mm embryo) from the internal maxillary artery (ramus infraorbitalis), in one case from the same vessel just where this gives off the arteria buccinatoria and in three cases it has a short common root with arteria buccinatoria springing from the internal maxillary artery. As arteria meningea media anterior must represent a part of ramus orbitalis and this ought to be a branch of arteria maxillaris interna, we have decided to consider this common root as a ramus orbitalis. Consequently the origination of the arteria meningea media anterior directly from arteria maxillaris interna must be regarded as a frequent irregularity. The very regular occurrence of the arteria meningea media anterior makes it probable that ancestors of Procavia have been provided with a well-developed ramus superior and ramus orbitalis, corresponding to the scheme proposed by TANDLER (1899) for Equus. A striking feature is the late appearance of the arteria meningea media anterior after the arteria buccinatoria has already reached a considerable length.

As in all Ungulates examined (TANDLER 1899) the arteria stapedialis disappears in Procavia its distal branches being taken over by arteria carotis externa. The connection is established by an anastomosis formed in two different pieces. The proximal end of this anastomosis originates primarily from the distal part of the external carotid but is then displaced proximally along this vessel. The distal end of the anastomosis joins the ramus mandibularis at some distance from the branching of arteria stapedialis. Thus a segment of the ramus mandibularis is added to the ramus infraorbitalis, both forming the arteria maxillaris interna. The borderline between these two elements is marked, however, by an arteria meningea media in all embryos that posses this vessel.

### On the arteria cerebri anterior.

The anterior cerebral arteries of Procavia run almost parallel rostrad in the earlier stages. Later they converge and give off large branches for the bulbus olfactorius and the nose and join their partners by the formation of primary anastomoses near the surface of the brain. These anastomoses run into the fissura longitudinalis forming an unpaired vessel, the rudiment of the arteria cerebri anterior communis on the bottom of the fissura. From the primary anastomoses, however, medialy directed branches are given off forming secondary anastomoses ventral to the mentioned ones and connected by a ventral

longitudinal vessel, the arteria cerebri anterior communis ventralis. This is reduced in the subsequent development as well as all accessory connections.

The developmental history of this junction is very similar to that described in Lepus by DE VRIESE (1907). There are some insignificant differences, the primary and secondary anastomoses being much more numerous in Lepus. Moreover, we have not been able to give any details of these parts of the vessels situated well in between the hemispheres. But there exists a more important difference. In Lepus the accessory longitudinal vessel is situated dorsal, in Procavia, on the other hand, ventral to the arteria cerebri anterior communis. The morphological significance of the accessory longitudinal vessel is, however, unknown.

## Comparative morphology.

JOLEAUD (1937) emphasizes the great individual variability of the skull bones and the hair colour in living Hyracoidea. Our studies have revealed a similar great individual variability of several arteries in the head of Procavia capensis. Striking also is the asymmetric development of some vessels, e.g. the ophthalmic arteries and the occipital arteries.

Our possibilities of comparing the arteries of Procavia with those of related mammals are rather limited since many structures are only described in domestic animals. For these we have mainly used the textbooks of ELLENBERGER and BAUM (1943) and SISSON (1927).

In Procavia the common carotid is split into external and internal carotids of about the same size, whereas the external carotid in Equus, Sus and the Carnivora is considerably larger than the internal one, which is lacking in Ruminatia. In this respect Procavia thus seems to be primitive.

The occipital artery originates in three different ways in mammals (cf. TANDLER 1899): 1. generally and especially in lower mammals from the carotis externa, this being the case in Equus, Bos, Capra and Ovis among ungulates; 2. from the carotis interna in Chiroptera and in single representatives of other orders: Sus (DIWO and KOTH 1913), Hyaena, Phoca, Erinaceus, Dasypus; 3. from the carotis communis, usually near its branching, in Orycteropus (SONNTAG 1925), Cervus, Camelus, several Carnivora, Cavia, Lemur, Otolicnus. In Procavia we find all these modes of origination if the developmental stages are also considered. In our embryos the occipital artery originates either from the external or the internal carotid. In the 80 mm embryo the vessel in question is on the left side, given off by the external and on the right side by the internal carotid. These conditions thus seem not to be fixed in Procavia. The instability of the occipital artery may possibly mean that this vessel is about to leave its connection with the external carotid typical of Ungulates and is to be taken over by the internal carotid, as has already happened



VOL
27
194

in Sus. For the adult Procavia, GEORGE (1874) states that the occipital artery is a branch of the common carotid and our older stages no doubt show a caudad displacement of its root in relation to the point of ramification of the common carotid. This ontogenetic displacement, which may also signify a fusion of the two carotids craniad as a similar displacement also occurs in the root of the lingual artery, probably reflects a corresponding phylogenetic displacement. We are consequently inclined to regard the origination of the occipital artery from the common carotid as a secondary condition also in other mammals.

Arteria maxillaris externa is rather poorly developed in Procavia and does not extend into an arteria facialis. In this respect it coincides with the same vessel in Sus which gives off branches to the glandula submaxillaris, musculus masseter, pterygoideus and mylohyoideus just as in Procavia.

The superficial temporal, the great auricular and the external maxillar arteries are branches of a common trunk in Procavia, which we have termed ramus externus of the external carotid. This arrangement seems to be unique, as these vessels originate separately from the external carotid in other mammals. In Procavia the ramus externus is given off as the next branch to arteria lingualis on the main trunk of the external carotid. In Sus, which has an external maxillary artery very similar to that in Procavia, the arteria maxillaris externa, arteria auricularis magna and arteria temporalis superficialis are the three most important vessels following the lingual artery. Equus and Bos are, as far as arteria temporalis superior and arteria auricularis magna are concerned, similar to Sus; the external maxillary artery differs, however, in that it gives off arteria alveolaris inferior and arteria lingualis.[1] The superior temporal, the great auricular and the external maxillary arteries originate from the external carotid at a comparatively small distance from each other. In Equus the distance between the superficial temporal and the great auricular arteries is very short, the two vessels having almost a common root. We thus find in the horse a tendency which has been completed in Procavia.

The trunk of ramus externus of the external carotid is probably homologous with the arteria auricularis magna, this being the first dorsally running vessel following the lingual artery in Sus. This suggestion is, however, not supported by the development; the first branch of the external carotid to develop after the lingual artery is sometimes the arteria temporalis superior and sometimes the arteria auricularis magna.

SICHER (1912) finds in Talpa that the arteria auricularis magna develops as a branch of the arteria stylomastoidea, which may be detected in very early stages running along the facialis nerve proximally posterior to the meatus auditivus externus. Similar conditions are reported in Sus by HOFMANN

[1] These arteries are very differently arranged in artiodactyle ungulates. However, Procavia and Sus seem to show primitive conditions.

(1914). In Procavia the great auricular artery has these relations, but the ramus externus of the carotis externa has not.

An interesting parallel to these conditions in Procavia is described by EALES (1926) in Elephas. The superficial temporal artery passing on the medial side of nervus facialis on its way to the lateral surface of the head has a common trunk with the great auricular artery which crosses the same nerve superficially. Although the relations to the facialis nerve are about the same as in Procavia, the common trunk does not take its origin from the external carotid but from arteria carotis communis. This discrepancy may be explained by the assumption that the common trunk is a secondary anastomosis, whereas the primary trunk has been reduced. Younger stages would here be of great interest.

Both an arteria facialis with its nasal branches and an arteria transversa faciei are absent in Procavia. Similar reductions have occurred in some Ungulates; Ovis and Capra lack the external maxillary artery. In Sus the arteria facialis is very poorly developed. Probably as a result of this reduction there appears in Procavia a vessel, arteria medialis nasi, as a branch from the internal carotid, providing the superficial parts of the nose. Since this vessel runs within the nasal bones in the adult it does, however, not provide the same layers as for example, the arteria nasalis dorsalis in Equus. As far as we have been able to ascertain, such a vessel has not previously been described.

In Procavia the arteria temporalis profunda is given off by the inferior alveolar artery in three cases of four. In the fourth (42 mm embryo) it takes its origin from the internal maxillary artery a short distance rostrally to the flexure of the latter corresponding in this respect to the single deep temporal artery in Bos and the aboral one in Homo, Equus, Sus, Canis and others.

With the exception of musculus oculi obliquus inferior, the eyeball and its extrinsic muscles are provided in Procavia by the ophthalmic artery. The "arteria ophthalmica externa", which both in the horse and the ruminants constitutes the main blood supply to the eye and its accessory organs, is thus missing in Procavia. Consequently an arteria ethmoidea externa is also missing in adult stages. In the 15.5 mm embryo, however, we have traced a small connection between the rete ethmoidalis and the arteries in the orbita. This is homologous with the large arteria ethmoidea externa in Equus, and with the smaller one in Sus.[1] The fact that this small vessel of Procavia joins in the orbit a branch of the arteria ophthalmica makes it probable that the present conditions are the result of a regressive development, an anastomosis between the internal maxillary and the ophthalmic arteries in the orbit having existed in earlier phylogenetic stages.

On comparing the meningeal arteries of Procavia with those of ungulates we find in the horse an arteria meningea media, which is sometimes double and

[1] In Bos the arteria ethmoidea externa does not form a connection with the rete ethmoidalis but runs through this.



VOL
27
194

enters the skull cavity through the foramen lacerum (ELLENBERGER and BAUM 1943). This corresponds in every respect to arteria meningea media in Procavia, the only difference consisting in a less regular occurrence of the latter. In the orbital region of the horse TANDLER (1899) describes an arteria meningea anterior[1] which he traces back to the ramus orbitalis. This vessel corresponds to the arteria meningea media anterior in Procavia. On the other hand there seems to be no arteria meningea media known in Bos as a branch of arteria maxillaris interna, the artery with this name being a branch on the arteria condyloidea and thus another vessel. When we turn to the pig as another representative of the Artiodactyla, we find an arteria meningea media described by SISSON (1927) as a branch of arteria maxillaris interna entering the cranial cavity through the foramen ovale. If this vessel, however, is identical with the arteria meningea whose development is described by HOFMANN (1914) in the pig, it cannot in its proximal part correspond to the arteria meningea media in other mammals. The condyloid artery seems to be the only caudal meningeal artery in Procavia.

The arteria cerebri anterior forms, as in the horse and the pig (HOFMANN 1900), an arteria cerebralis anterior communis. In Cervus, Capra, Ovis and Bos this junction is represented by a vascular fine-meshed net joining the two arteries (HOFMANN 1900). This may represent a more primitive phylogenetic stage which is passed by Procavia during its development. The ramus ethmoidalis of the arteria cerebri anterior forms a large and very long vessel. According to HOFMANN (1900) this vessel is totally lacking in Cervus, has been observed twice on one side in juvenile specimens of Bos as a rather small vessel, is present in Sus and constitutes a large vessel in Equus. It occurs in all the Carnivora examined by HOFMANN (Canis, Lutra, Mustela, Felis) but seems to be lacking in other orders of mammals. The arteria ethmoidalis communis seems to be a structure unique to Procavia. Of arteria bulbus olfactorius medialis and lateralis, which are both present in all the four above-mentioned ungulate genera, the former occurs in some Procavia embryos in a more or less complete state. It seems to be in regression and is replaced by the arteria bulbi olfactorii anterior originating from ramus ethmoidalis. The other artery is lacking in Procavia.

Since the posterior portion of the arteria ethmoidea externa does not occur, its nasal portion is also lacking. Thus the nasal cavity is furnished only by the arteria sphenopalatina and branches of arteria cerebri anterior.

The ophthalmic artery originating from arteria cerebri anterior is a very large vessel which provides the eye-ball and its extrinsic muscles with the

[1] In view of the application of the term arteria meningea anterior to ramus ethmoidalis in the horse (FRANK 1894) and to a small branch of the anterior cerebral artery in the same animal (SISSON 1927), we have avoided this term, instead calling the vessel corresponding to the ramus orbitalis, arteria meningea media anterior.



VOL. 27 1946

exception of musculus obliquus inferior. In all ungulates examined, however, this artery seems to be highly reduced (HOFMANN 1900; TANDLER 1899, 1901; ELLENBERGER and BAUM 1943). It originates in the horse and some Artiodactyla from the anterior cerebral artery just where this is given off and in other Artiodactyla from the same artery at some distance from the branching of the internal carotid. In contradistinction to this, arteria ophthalmica is the only vessel providing the orbit in man and in some Marsupials (Halmaturus, Macropus).

According to HOFMANN (1900) arteria cerebri media divides into three branches in all the mammals studied by him, with the exception of Homo and Sciurus. In Procavia only two branches are said to occur (GEORGE 1875). As we have not followed the posterior cerebral artery and its branches we are not able to classify it according to LEHMANN. Its mode of origination and its immediate division makes it probable that it corresponds to arteriae cerebri posterior $\beta$ and $\delta$. The anterior cerebellar artery is an arteria cerebelli $\alpha$ and the posterior cerebellar artery is an arteria cerebelli $\gamma$ according to HOFMANN's terminology. These two vessels cooperate in providing the cerebellum in Lepus, Erinaceus, Lutra, Sus and Equus but not in Bos.

Concerning the relations between the occipital, vertebral and basilar arteries we were not able to confirm the statements of GEORGE as we could trace no connection either between the occipital and the vertebral arteries on the one hand or between the occipital and the basilar arteries on the other. Instead we found the arteria vertebralis to be connected with the basilar artery by its third ramus spinalis running between the axis and the third vertebra. This connection is rather variable in the Ungulata. In Sus and Equus arteria vertebralis and arteria occipitalis join and send the arteria cerebrospinalis (as first ramus spinalis) through the foramen intervertebrale of the atlas to the basilar artery, just as reported by GEORGE for Procavia. In Bos the arteria vertebralis sends a vessel either between the second and third (third ramus spinalis) or between the third and fourth vertebrae (fourth ramus spinalis) into the vertebral canal. In the atlas this vessel forms an anastomosis with the occipital artery through the invertebral foramen of this vertebra and enters into connection with the rete mirabile epidurale of the internal carotid. In Felis and Canis exist both the connection through the foramen intervertebrale of the atlas and between the second and third cervical vertebra. Since we cannot entirely exclude the possibility, however, that the connection between the basilar artery on the one hand and the occipital and vertebral arteries on the other is formed in the postnatal development, which would make the adult Procavia conform to the mentioned Carnivora, it is advisable not to enter into further comparisons.

Summing up we find that the arteries in the head of Procavia have preserved many primitive features as have also those of the horse. In details they show



VOL
27
194

similarities to those of most Ungulata. Besides these primitive features we may note reductions of the vessels of the face and the occurrence of some structures which seem to be special to Procavia.

## SUMMARY.

1. The aortic sac in mammals is to a great extent formed by fusion of the caudal ventral aortae. In some mammals that are to be considered less primitive, this fusion takes place immediately after the formation of the vessels, in others it is delayed, so that the paired state remains until a later stage.

2. As the fourth aortic arch of Procavia is partly double in early stages, it is suggested that this corresponds to the fourth and fifth arches in reptiles. Since the "provisional fourth" arch disappears, the definitive fourth arch may represent a reptilian fifth arch.

3. A "provisional sixth" arch, probably corresponding to the dorsal root of the sixth arch of reptiles and connected with the dorsal aorta, occurs in Procavia and, to judge from TANDLER's (1902) account, also in Mus. In Procavia its caudal portion disappears, the cranial probably forming the dorsal root of the pulmonary arch, whereas the reverse takes place in Mus. Because of its presumed phylogenetic significance the term "prepulmonary arch" is proposed for this structure.

4. The dorsal root of the pulmonary arch has a short common trunk with the fourth aortic arch in Procavia as in man. This common trunk, unlike that in Procavia, soon disappears in man.

5. It is pointed out that the so called fifth arch of mammals runs in many cases laterally to the ultimobranchial body, as do the reptilian sixth arch and the prepulmonary arch. The possibility of introducing these elements into the discussion is suggested.

6. A first generation of longitudinal neural arteries in very intimate contact with the brain surface is replaced by a second generation at some distance from this surface. The primary neural arteries have ventrally directed protrusions, extending in their end parts rostrocaudad, joining together and forming a new longitudinal trunk, which is connected with the primary neural by numerous anastomoses. Then the primary neural is obliterated.

7. In Procavia the two longitudinal neural arteries approach mutually before forming the basilary artery. Probably in consequence of this, the disintegration of segments of the neurals does not play here such a great rôle in the formation of the basilar artery as in man.

8. As in man, and contrary to what happens in many other mammals, the external carotid artery is formed as a new vessel, situated at the third aortic arch near the origin of the latter.

9. Of the three branches of the stapedial artery only ramus infraorbitalis is laid down as a continuation of the first aortic arch, the ramus superior and ramus inferior being formed as sprouts of the stapedial artery. In this respect Procavia is similar to the primitive lacertilian Platydactylus. Ramus superior is very small and its occurrence irregular. The anterior branches of the stapedial artery are taken over by the external carotid.

10. A comparison with Ungulata in respect of the head arteries in the adult shows that Procavia has preserved many primitive features. In Procavia the reduction of the face arteries has proceeded very far. Procavia also posesses some special structures.

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VOL.
27
194

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VOL.
27
1946

## EXPLANATION OF LETTERINGS.

*al.i.*, arteria alveolaris inferior.
*al.i.p.*, arteria alveolaris inferior primaria.
*al.i.s.*, arteria alveolaris inferior secundaria.
*al.s.*, arteria alveolaris superior.
*an.*, anastomosis between ramus mandibularis and external carotid
*a.s.*, aortic sac
*a.tr.*, aortic trunc.
*b.*, arteria basilaris.
*buc.*, arteria buccinatoria.
*c.*, arteria condyloidea.
*c.a.*, arteria cerebri anterior.
*ca.i.*, ramus caudalis of internal carotid
*cb.a.*, arteria cerebellaris anterior.
*cb.p.*, arteria cerebellaris posterior.
*c.c.*, arteria cerebri anterior communis.
*c.com.*, arteria carotis communis.
*c.e.*, arteria carotis externa
*c.i.*, arteria carotis interna.
*c.m.*, arteria cerebri media.
*com.p.*, arteria communicans posterior.
*c.p.*, arteria cerebri posterior.
*cr.i.*, ramus cranialis of internal carotid
*d.a.*, dorsal aorta.
*d.c.*, ductus caroticus.
*e.*, arteria ethmoidalis.
*e.c.*, ramus externus of external carotid.
*et.*, ramus ethmoidalis.
*et.c.*, arteria ethmoidalis communis.
*h.*, arteria hyoidea.
*i.*, ramus inferior of arteria stapedialis.
*io.*, arteria infraorbitalis.
*i.o.s.*, ramus infraorbitalis of arteria stapedialis.
*l.*, arteria lingualis.
*m.*, ramus mandibularis.
*m.a.*, meningea media anterior.
*mal.*, ramus malaris.
*md.n.*, arteria medialis nasi.
*m.m.*, arteria meningea media.
*mu.*, ramus muscularis of arteria occipitalis.
*mx.e.*, arteria maxillaris externa.
*mx.i.*, arteria maxillaris interna.
*n.l.*, arteria neuralis longitudinalis.
*n.l.p.*, arteria neuralis longitudinalis primaria.
*n.l.s.*, arteria neuralis longitudinalis secundaria.
*N.p.*, nervus petrosus superficialis major.
*n.p.l.*, arteria nasalis posterior lateralis.
*n.p.s.*, arteria nasalis posterior septi.
*N.V.1.*, ramus ophtalmicus of nervus trigeminus.
*N.V.2.*, ramus infraorbitalis of nervus trigeminus.
*N.V.3.*, ramus mandibularis of nervus trigeminus.
*N.VII.*, nervus facialis.
*o.*, arteria occipitalis.
*oph.*, arteria ophtalmica.
*or.*, ramus orbitalis.
*p.*, arteria pulmonalis.
*p.a.*, pulmonary arch.
*ph.c.*, caudal pharyngeal complex.
*p.m.*, arteria palatina major.
*pp.a.*, prepulmonary arch.
*p.tr.*, pulmonary trunc.
*s.*, ramus superior of arteria stapedialis.
*sc.*, ramus septalis of arteria ethmoidalis
*sp.*, arteria sphenopalatina.
*st.*, arteria stapedialis.
*t.-l.*, arteria thyreo-laryngea.
*t.p.*, arteria temporalis profunda.
*tr.a.*, truncus arteriosus.
*t.s.*, arteria temporalis superficialis
*v.a.*, posterior ventral aorta.
*I—IV*, first to fourth aortic arch.
"*IV*"—"*V*", fourth to fifth provisional arch.
*1*, hyoid.
*2*, stapes.
*3*, processus alaris.
*4*, ala temporalis.
*5*, foramen opticus.
*6*, fissura orbitonasalis.
*7*, cartilago paraseptalis.
*8*, processus paracondyloideus.
*9*, cartilago Meckelii
*10*, auditory capsula.
*11*, septum nasi.

OL.
27
946

VOL
27
194

# ASCOTHORAX OPHIOCTENIS AND THE POSITION OF ASCOTHORACIDA WAGIN IN THE SYSTEM OF THE ENTOMOSTRACA

BY

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CONTENTS.

I. Introduction . . . . . 156
II. Historical survey . . . . . 157
III. Material and method of investigation . . . . . 161
IV. Description of Ascothorax ophioctenis . . . . . 162
A. The external anatomy, segmentation and size . . . . . 162
a) The shape and size of the body . . . . . 162
b) Pigmentation. The colour of the body . . . . . 165
c) The mantle . . . . . 165
d) The segmented body . . . . . 167
e) The cephalic appendages . . . . . 169
1) The antennules . . . . . 169
2) The oral pyramide . . . . . 172
f) The appendages of the thoracic portion . . . . . 174
B. The internal anatomy . . . . . 176
a) The integument . . . . . 176
b) The nervous system and organs of sense . . . . . 176
c) The gut . . . . . 179
d) The muscles of the body proper . . . . . 184
e) The connective tissue . . . . . 187
f) The lacunary system . . . . . 188
g) The excretory system . . . . . 188
h) The reproductive system . . . . . 189
i) An unknown glandular organ in females . . . . . 191
C. Development . . . . . 192
a) The fertilization and the laying of the eggs . . . . . 192
b) The nauplius . . . . . 193
c) The metanauplius . . . . . 194
d) The ascothoracid stage . . . . . 194
D. The relation of parasite to host . . . . . 200

V. Comparative survey of the Ascothoracida . . . . . 206
A. The body form, segmentation and appendages . . . . . 206
a) The bodyform and the mantle . . . . . 207
b) The segmented body . . . . . 209
B. The appendages . . . . . 210
a) The antennules . . . . . 210
b) The antennae . . . . . 215
c) The oral apparatus . . . . . 216
d) The appendages of the thoracic portion . . . . . 218
C. Anatomy . . . . . 220
a) The integument . . . . . 220
b) The nervous system and the organ of sense . . . . . 221
c) The alimentary system . . . . . 222
d) The muscles of the body . . . . . 224
e) The connective tissue and the lacunary system . . . . . 225
f) The excretory system . . . . . 225
g) The reproductive system . . . . . 226
h) Fertilization . . . . . 230
D. The larvae . . . . . 230
a) The Nauplius stage . . . . . 231
b) The Ascothoracid larvae . . . . . 232
E. The relation of parasite to host . . . . . 233
F. The relation between the sexes . . . . . 236
G. Geographical distribution . . . . . 239
H. The phylogeny of the Ascothoracida . . . . . 240
I. The position of Ascothorax ophioctenis in the system of Ascothoracida . . 245
VI. The position of the Ascothoracida in the system of Entomostraca . . . . . 246
A. A comparison with the Cirripedia . . . . . 246
B. A comparison with the Copepoda . . . . . 253
C. The position in the system . . . . . 260
VII. Summary . . . . . 262
Literature cited . . . . . 264

VOL
27
194

## I. INTRODUCTION.

The specimens of Ascothorax ophioctenis Djakonov which have served as material in the present investigation were collected by me in the Kara Sea during the expeditions of the All Union Arctic Institute. In the summer of 1933 the material was secured by the ice breaker "A. Sibiryakov" in the region of the Nordenskiöld Archipelago and in 1934 by the ice breaker "G. Sedov" in the northern and northeastern area of the Kara Sea.

The systematic position of the Ascothoracida lacks in clearness as this group is in many respects peculiar and presents a great interest from the standpoint of comparative anatomy and phylogenetics; this as well as the fact that we possess but a scant knowledge of Ascothorax ophioctenis were the cause of my undertaking these researches.

In the spring 1934, having started the examination of the material collected, and wishing to verify my determinations, I applied to the Zoological Institute of the USSR Academy of Science and to A. M. Djakonov by whom this

interesting parasite had been discovered and described. By courtesy of A. M. DJAKONOV I have been able to compare the type specimens of the Museum with my own and thus to assure myself of their full identity. I am also greatly beholden to A. M. DJAKONOV for having kindly put at my disposal his drawings and notes relating to these forms.

The data I have obtained relating to the inner anatomy of Ascothorax ophioctenis are wholly new, and I have been able to considerably enlarge and render more complete the existing descriptions of their external anatomy. Besides evidence was obtained that the present standpoint respecting the systematic position of the Ascothoracida is erroneous. Up to the present time the Ascothoracida are placed in the Cirripedia. They are considered to represent a suborder—namely Cirripedia Ascothoracica Gruvel 1905. But the study of the morphology of this group and especially the study of their larvae have given to recognise that the Ascothoracida form a separate order, phylogenetically closely related to the Cirripedia.

VOL. 27 1946

The investigations were begun in the Laboratory of Zoology of Invertebrates in the State University, Leningrad. The work was carried on, brought to a close and written in the Laboratory of the Department of General Biology of the Second Leningrad Medical Institute.

The writer desires to record his gratitude to his teachers—Prof. V. A. DOGIEL, Prof. P. P. IVANOV and Dozent A. P. RIMSKY-KORSAKOV of the Laboratory of Invertebrates; their valuable advice has greatly helped me in the course of my investigation. Acknowledgments are due also to Prof. B. N. SCHWANWITSCH, to A. V. IVANOV and those of my colleagues in the laboratory who have shown a warm interest in my work.

## II. HISTORICAL SURVEY.

The investigations on Ascothoracida were started by LACAZE-DUTHIERS who was the first to discover and to describe—in 1866—a specimen of this group. In 1883 this author published a monographic description of the form discovered —Laura gerardiae, an endoparasite of the coral Gerardia. In it he treats of the structure, plan, and the development of Laura gerardiae. Of the highest import is LACAZE-DUTHIERS indication of his findings of a cypris—like organism which he considers as a cypris larva. The cypris "larva" and the sac-like mantle of the adult Laura caused LACAZE-DUTHIERS to place the Ascothoracida—(the Rhizothoracida) as he named them—in the Cirripedia abortiva which included our group, and the Rhizocephala. In Cirripedia vera according to this investigations were included the Thoracica and the Abdominalia (the Acrothoracica of the presentday system).

*Petrarca bathyactidis* was described by FOWLER in 1890. This Crustacean parasitates in the gastral cavity in the deep sea corall Bathyactis symmetrica.

1892 appeared the dissertation of N. M. KNIPOWITSCH on Dendrogaster astericola—a parasite of the body cavity of the starfish Echinaster sanguinolentus. This parasite was described by KNIPOWITSCH in 1889. His dissertation treats of the morphology and development of the parasite. These questions are discussed by the author in the first two chapters. KNIPOWITSCH also investigated a new specimen of Laura gerardiae which the author had obtained from LACAZE-DUTHIERS. In his last chapter the author gives a comparative survey of the group Ascothoracida in which he compares the various representatives of the group with each other, as well as with nearly all the groups belonging to the Entomostraca. Further the author denoted the characteristic features of Ascothoracida and mentions a number of peculiarities in which they differ from the Cirripedia. However he does not consider these forms as a separate order, but leaves them in the Cirripedia group, putting them in a special suborder and contrasting them against all the other Cirripedia.

A comprehensive symposium on Cirripedia by GRUVEL was published in 1905. In this monographical treatise its author makes a revision of the system of Cirripedia and the systematic position of the group, which, like DARWIN, he considers to be not an order, but a subclass represented by five orders: Thoracica, Acrothoracica, Ascothoracica, Rhizocephala and Apoda. In the Ascothoracica GRUVEL distinguishes the families: Synagogidae, Lauridae, Petrarcidae and Dendrogasteridae.

In the same year LE ROI published a preliminary report and two years later—in 1907—he gave a detailed morphological examination and description of two new species of Dendrogaster: D. arborescens and D. Ludwigi (these two species were in after years put into another genus—Myriocladus Okada).

In 1912 NORMAN gave a detailed description of the habitus of Synagoga mira—an ecto-parasite of the coral Antipathes laris Ellis, which the author had discovered in 1887.

A preliminary report by DJAKONOV treating of Ascothorax ophioctenis—parasite of bursal cavities of the brittle-star Ophiocten sericeum Forbes—was published in 1914. DJAKONOV considers this form as belonging to the family Synagogidae Gruvel.

In 1925 a special genus named Myriocladus was established by OKADA for the family Dendrogasteridae, and a year later the same author gave a description of Synagoga metacrinicola—a new species parasitating on the inside of the disc of the Crinoid Metacrinus rotundus Carpenter.

A new genus of the family Lauridae Gruvel—Baccalaureus—was described by BROCH in 1929. These are parasites of the corals Gorgonaria.

In 1931 two articles were published by JOSII: 1) A systematic survey of the genus Myriocladus Okada together with a description of two new species of the genus (M. Okadai and M. astropectinis), and 2) a monographic survey and more complete description of Baccalaureus japonicus found by BROCH. This paper contains the first reliable description of the males which for the family Lauridae were known only by the drawing given in the work of LACAZE-DUTHIERS who took them for cypris-like larvae.

1933 KORSCHELT, in his article on parasitic Cirripedia, treats of two insufficiently known representatives of the genus Dendrogaster (D. murmanensis Klugge n. nud. and D. arcticus, which FISCHER in 1930 had described as Dendrogaster sp.).

A new species of the genus Baccalaureus—B. maldivensis was described by PYEFINCH in 1934, and two years later the same author published a description of yet another species—Baccalaureus hexapus. The paper contains a morphological and histological description of this form. Both these species are parasites of corals—Gorgonaria and Zoantharia.

In 1935 STEPHENSON published an investigation on the systematics of Ascothorax ophioctenis Djakonov; the material he employed was secured by the "Ingolf" expedition.

Towards close of the year 1936 appeared a preliminary report by BRATTSTRÖM in which a new genus of the family Dendrogasteridae—the most primitive of all the genera known—is described. The author named it Ulophysema. U. öresundense Bratt. parasitates in the coelome of Echinocardium cordatum (Pennant). Another species of this genus—U. pourtalesiae was described by BRATTSTRÖM in 1937—it is a parasite of the body cavity of Pourtalesia jeffreisi W. Thomps.

This seems to be a complete chronological list of the principal works treating of the description of the representatives of Ascothoracida. In 1937, towards close of the year, appeared PYEFINCH's paper containing the description of a new species—Baccalaureus torrensis, a parasite of Polythoa from the Torres Strait. And three species from Zansibar in 1939: B. digitatus, B. verrucosus and B. disparcaudatus.

The most comprehensive are the works of LACAZE-DUTHIERS (1888), of KNIPOWITSCH (1892), LE ROI (1907) and JOSII (1931).

The number of representatives of the Ascothoracida is not large. At the present moment we know 23 species which—according to GRUVEL's system—are comprised into four families and seven genera of the suborder Cirripedia Ascothoracica Gruv.

## Ordo Cirripedia.
## Subordo Ascothoracica (Gruvel 1905)

### Fam. Synagogidae Gruv. 1905.

*Gen. 1. Synagoga Norman.*
spec. 1. S. mira Norman 1887.
„ 2. S. metacrinicola Okada 1926.

*Gen. 2. Ascothorax Djakonov.*
spec. 3. A. ophioctenis Djakonov 1914.

### Fam Lauridae Gruv. 1905.

*Gen. 3. Laura Lacaze-Duthiers.*
spec. 4. L. gerardiae L.—D. 1866.

*Gen. 4. Baccalaureus Broch.*
spec. 5. B. japonicus Broch 1929.
„ 6. B. maldivensis Pyefinch 1934.
„ 7. B. torrensis Pyefinch 1937.
„ 8. B. hexapus Pyefinch 1936.
„ 9. B. argalicornis Brattström 1936.
„ 10. B. verrucosus Pyefinch 1939.
„ 11. B. disparcaudatus Pyefinch 1939.
„ 12. B. digitatus Pyefinch 1939.

### Fam. Petrarcidae Gruv. 1905.

*Gen. 5. Petrarca Fowler.*
spec. 13. P. bathyactidis Fowler 1890.

### Fam. Dendrogasteridae Gruv. 1905.

*Gen. 6. Ulophysema Brattström.*
spec. 14. U. öresundense Brattström 1936.
„ 15. U. pourtalesiae Brattström 1937.

*Gen. 7. Dendrogaster Knipowitsch.*
spec. 16. D. astericola Knipowitsch 1890.
„ 17. D. arcticus Korschelt (Fischer) 1930.
„ 18. D. murmanensis Kluge 1910 n. nud.

*Gen. 8. Myriocladus Okada.*
spec. 19. M. okadai Josii 1931.
„ 20. M. astropectinis Josii 1931.
„ 21. M. arborescens Le Roi 1905.
„ 22. M. Ludwigi Le Roi 1905.
„ 23. M. arbusculus Fischer 1911.



VOL
27
194

In the present day system of Cirripedia the suborder Ascothoracica (Gruvel 1905) is put between Acrothoracica (s. Abdominalia) and Rhizocephala. This is where GRUVEL places them in his system of Cirripedia.

This system is at present generally accepted with that difference that the Cirripedia are considered to represent an order and not a subclass, as we find in GRUVEL's Monography of 1905.

## III. MATERIAL AND METHOD OF INVESTIGATION.

The Ophiurae infested with Ascothorax ophioctenis were secured during the sampling and counts of the trawling material in which Ophiocten sericeum occurred in large numbers. It was not infrequent that some 10.000 specimens of this brittle-star were counted and in one instance above 17.000 specimens were secured. The ophiuroids being so numerous, their sampling, as the work permitted of no dealy, the selection of infested specimens, presented great difficulties. Consequently the probability is that not all the infested Ophiurids were secured—many must have escaped attention, especially such as were inhabited by parasites in their juvenile stage.

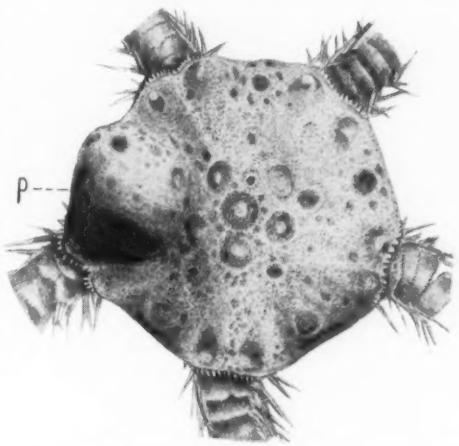


Fig. 1. Ophiocten sericeum infested with Ascothorax ophioctenis, general view. Magnif. 4 ×. *P*—swelling caused by the parasites.

The presence of Ascothorax ophioctenis was recognisable by swellings of the disc of Ophiocten sericeum, in the interradius, at the base of one of the rays (fig. 1). Some of the infested brittle-stars were opened and their parasites extracted; in others the parasites were taken together with a portion of the host's body. In the latter case the envelope about Ascothorax ophioctenis was only slightly burst open so as to prevent the falling off of the small males sitting with the female. This precaution was taken with the purpose of making possible, in the subsequent laboratory investigations, the rating of males against females. Further, infested ophiurans were fixed in toto—this material permitting to establish the exact location of the parasite within the body of the host and likewise helping to solve various other questions.

The Ophiurids were opened with needles, the object lying on the stage plate of the lens microscope. After the animals had been opened the objects were fixed, for which various fixing agents were employed: 1) sublimate dissolved

in sea water, with acetic acid (5:1) hot; 2) hot GILSON's solution in A. RIMSKY-KORSAKOV's modifikation; 3) the ZENKER-HELLY solution—both hot and cold, 4) FLEMMING's strong formula. The type specimen were preserved in alcohol of 70 %. The best results were obtained with the FLEMMING formula and the GILSON solution. Fixations with ZENKER-HELLY, and sublimate plus acetic acid also were quite acceptable, but proved to be somewhat less good than the above mentioned methods.

The investigations were continued in Leningrad under laboratory conditions: total drawings were traced, preparations in toto, and serial sections, as well as preparations of the parasites' limbs were made. The examination of the chitinous parts was carried out on objects boiled in a 10 % solution of KOH. For the preparations of the limbs in toto inclusion in a glycerin-gelatine mixture was practised. These preparations did not take up much time; they were found to be very clear permitting to easily distinguish the topography of the musculature in the limb. For the study of the topography of the receptaculum seminis isolated thoracopodia were stained with picro-carmine and included in Canada balsam.

The anatomy of the parasite was studied on sections. According to the purpose of the investigation the sections were of a varying thickness—from 7.5 to 15 $\mu$. The topography of separate organs was studied by means of graphical reconstructions. Various stains were employed—borax carmine, HEIDENHAIN's iron hematoxyline with subsequent staining with eosine or a mixture of aniline blue and orange G, while for rough anatomical purposes the triple stain of Mallory was employed.

The minute orientation necessary for reconstructions was made on celloidin plates. The embedding was done after PETERFI's method by way of a celloidin-paraffin mixture.

When orientating the sections we either guided ourselves by parallelly cut borders of the plates, or parallelly disposed muscular fibres, or nerves of frogs were embedded together with the object.

## IV. DESCRIPTION OF ASCOTHORAX OPHIOCTENIS.

### A. THE EXTERNAL ANATOMY, SEGMENTATION AND SIZE.

Each infested bursa contains: one large female and one or more males (fig. 2). The males differing from the females in their size and various other features (fig. 3) the male and female forms are always described separately.

#### a. The shape and size of the body.

The female when freed of the tissues of the host is, by reason of the strongly developed mantle valves, slightly heartshaped or nearly spherical in form. Its



VOL
27
194

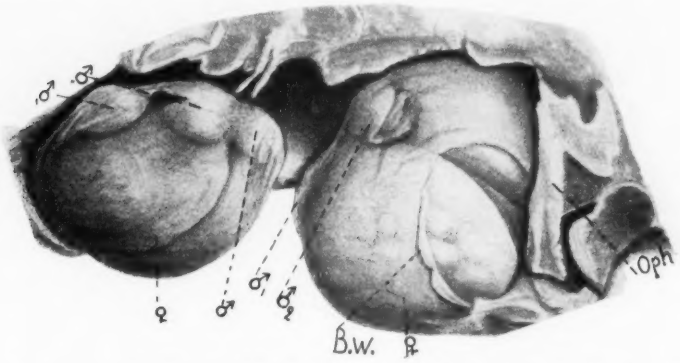


Fig. 2a. The same as in fig. 2. with that difference that here a simultaneous infestation of two bursae is reproduced. One bursal wall is opened and the localisation of the parasites that lie immediately below it comes into view. Magnif. 12 ×. *B.W.*—Bursal wall; ♀—female; ♂—males.

VOL. 27 946

anterior end is slightly tapered. A deep furrow runs along the median line of the dorsal side, ending on the ventral side; it terminates as the mantle aperture. Through this aperture the antennulae and the hind end of the abdomen with its furca may frequently be seen (fig. 4). This shape of the body is due to the strong development of the mantle valves within which besides the gonads and the ramifications of the intestine, a large brood pouch is contained.

The valves of the mantle fuse together on the dorsal side by means of a short dorsal suture. The presence of the gonads and the brood pouch in the valves causes these to grow in size not only in the lateral direction but also upwards. Thus the valves without fusing mount upwards from the dorsal suture and form a longitudinal dorsal furrow (fig. 3). The dorsal suture commences at the anterior end of the mantle slit and terminates at the dorsal surface of the first thoracomere. The other portions of the edges are free.

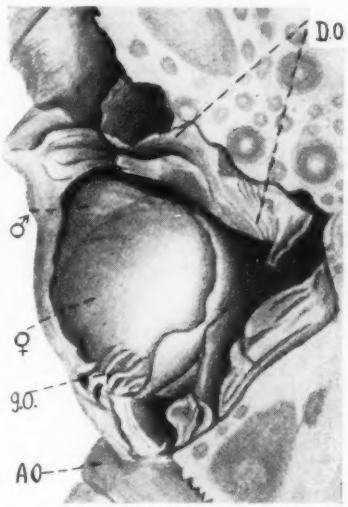


Fig. 2. Part of a sectioned Ophioctenis sericeum. Within its bursa—a male ♂ and a female ♀ Ascothorax. Magnif. 8 ×. *A.O*—arm of the ophiurid; *D.O*—intestine of the ophiurid; *G.O*—gonads of the ophiurid—the slight development of the gonads is to be noted.

Between the valves of the mantle lies a segmented body which coalesces with the valves by the dorsal and lateral area of its cephalic portion and the anterodorsal area of the first thoracic segment. It is distinctly segmented and consists

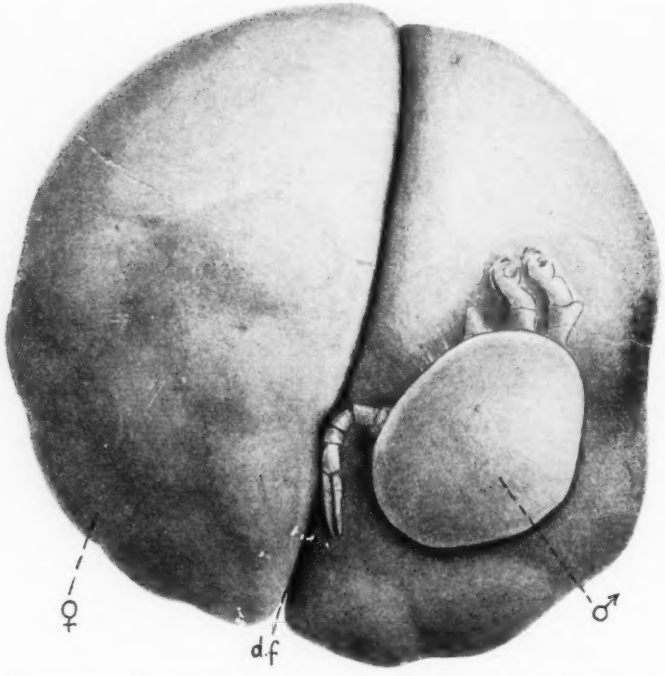


Fig. 3. Male and female Ascothorax taken out of the host—the female is seen from the dorsal side. Magnif. about 30 ×. *d.f*—dorsal longitudinal furrow between the valves.

of three typical portions: head, thorax, and abdomen. The size of the female animal, when measured together with its valves is not above 2.8 mm in length. Larger specimen measuring 3.5 mm as well as smaller specimen of from 1.5 to 1.8 mm may occur—but they are an exception. Their breadth varies greatly and reflects the state of the brood pouch—the degree of its distention.

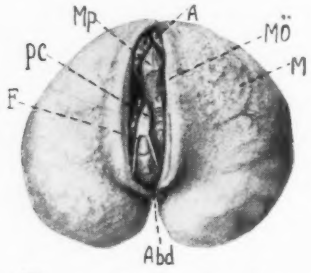


Fig. 4. Female Ascothorax viewed from the ventral side. Through the mantle aperture the body of the Crustacean is visible. Magnif. about 12 ×. *A*—antennules; *Abd*—abdomen; *F*—furca; *M*—mantle; *Mö*—mantle aperture; *Mp*—oral pyramid; *p.c.*—conial excrescence on the V abdominal segment.

The external anatomy of the male differs widely from that of the femals; they are thickly beanshaped. The mantle valves are not very strongly developed; they scarcely cover the body of the male and—as in females—are joined together by a short dorsal suture leaving the main portion of the borders of the valves free. The valves are fairly massive as they contain the testes and the ramifications of the intestine (fig. 5). As in females the body of the male fuses with the the mantle in its cephalic portion and the anterior portion of the first thoracomere. As in females also head, thorax and abdomen may be

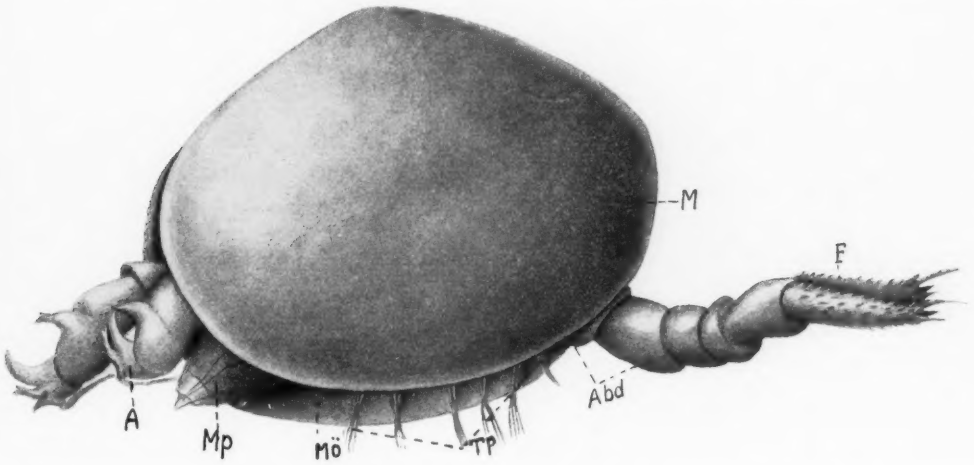


Fig. 5. General view of the male Ascothorax. Magnif. about 60 ×. *Tp*—thoracopodia; the other lettering as in fig. 4.

distinguished, the segmentation is more distinct. The size of the males varies from 0.4 to 1.2 mm of valve length, the height of the valves amounting to about 2/3 of their length.

### b. Pigmentation. The colour of the body.

The live Ascothorax ophioctenis are of a bright orange colour. The females are of a brighter colour and in them the colouring is irregularly distributed. Most intensely coloured is the anterior part of the mantle which bears the branches of the gonads and the intenstine. The portion containing the brood pouch is paler, the colour of this portion depending on the colour of the embryos and larvae with which it is filled. The empty brood pouches are nearly white.

The males have a more even colouring which at the same time is less bright.

### c. The mantle.

The mantle, or carapax is the strongly grown carapax of the nauplius. The structural features of the mantle in Ascothorax ophioctenis represent a secondary sex character. The half spherical mantle valves in the females are not homogeneous in their structure and consist of two portions—a massive anterior and a posterior thin walled portion. The massive portion includes the anterior and the ventral parts of the valve; it produces along the whole of the ventral margin a bolsterlike swelling which is thickest along the posterior ventral margin of the valves (fig. 6), in the place where it continues onto the dorsal side. Within the massive portion lie the branches of the gonads and of the

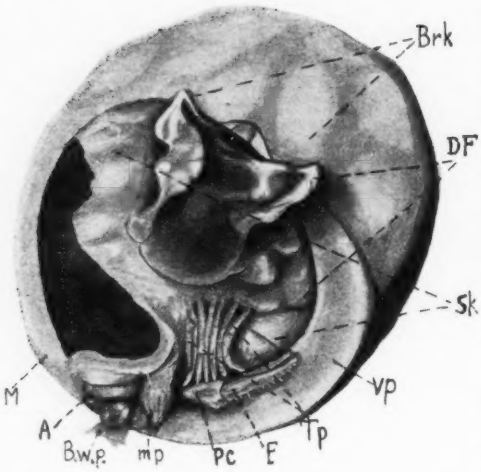


Fig. 6. Female Ascothorax with the right side of the mantle removed making visible the segmented body. Magnif. 16 ×. *Brk*—brood pouch; *Bwp*—portion of the bursal wall grasped by the antennule; *DF*—dorsal processes; *SK*—segmented body; *Vp*—ventral bolster-like swelling. In black—the place of fusion of the body with the mantle. The other lettering—as above.

intestine. The free spaces between these organs are filled up with loose connective tissue forming a network of lacunes which is particularly thick about the ovaries and the gut diverticula. In the bolster-like swelling the branches of the intestinal ducts are ubiquituous, while the ovaries lie only in the ventral portion of these swellings.

The posterior thinwalled portion in adult females fills the major part of the valves. It forms large sac like swellings—brood pouches—in which the embryos are incubated and the development of the larvae up to the Ascothoracid stage takes place. In most females this cavity is filled with young various stages of development. Females with an empty brood pouch occurred rarely.

The *walls of the brood pouch* differ structurally from the massive portion. The gut diverticula and the gonad do not reach into it. All the space lying between the covering layers is filled with loose connective tissue, in the meshes of which a network of variously sized lacunes is disposed (fig. 5, plate I).

Moreover, the walls of the brood pouch contain a special musculature consisting of *a middle layer* of fibres intersecting at a sharp angle—it occupies the middle portion of the brood pouch wall and is parallel to the wall surfaces —and of transverse muscular fibres running from the external to the internal surface of the brood pouch wall. The disposition of the musculature and the wrinkled aspect of the empty brood pouches clearly show that these walls have the ability to contract and change their shape.

In males the valves of the mantle are homogeneous and are massive throughout. Within them lie the lobes of the testes and the branches of the gut diverticula. As in the female, the spaces between the organs are filled up with loose connective tissue containing a network of lacunes. The *musculature* is very simple, it consists of transverse muscular bundles running from the one wall of the valve to the other. The transverse muscles serve to produce a flattenning of the valves this being necessary for maintaining the flow of fluid in the lacunes. They play presumably a similar rôle in the walls of the brood pouch of the females.

### d. The segmented body.

As mentioned above, in the segmented body a cephalic, a thoracic and an abdominal portion may be distinguished. On the whole the body consists of 16 segments, part of which (the cephalic segments) are fused together. In males the segmentation is distinct, more so than in females—in these the orientation and the shape of the body are adapted to the incubation of the embryos. Likewise, as will be seen further on, the sexual dimorphism is expressed in the structure of the limbs.

The body of the female is considerably smaller than the valves, it lies between them and is always curved in the form of the letter S (fig. 6). The number of segments in the body is constant, and amounts to 16: the cephalic portion consists of 5 segments fused together; four of these possess shears like antennulae (the first antennae), and three pairs of mouth appendages included as in a sheath in the upper lip. Because of this the whole oral apparatus presents the aspect of a cone, or more exactly, beeing of triangles shape—of a pyramid, thence the designation oral pyramide, or oral cone. The adult Ascothorax ophioctenis posses no second antennae.

The thoracal portion consists of six distinct segments—of these five segments posses each one pair of biramous leafshaped limbs, while the first segment bears a pair of uniramous leafshaped appendages.

In the dorsal side of the thoracic portion, in the female, four pairs of conical processes are present; they are directed upwards and somewhat sideways so that they are nearly wholy included in the brood pouch of the mantle valves. These excrescences belong to the 3, 4, 5 and 6 thoracic segments. The first two excrescences are very large and taper to a simple pointed end, while the third and fourth are considerably smaller and are split at the apex (fig. 6). STEPHENSEN (1935) represents in a drawing and describes two pairs of excrescences only, namely the first and the second pair which are the largest (see his fig. 2, p. 4).

The presence of an abundant musculature in these processes leads us to conclude that on the one hand they possess a certain mobility, and on the other hand the muscles act as a resilient support of the valves filled with larvae, this being presumably the principal rôle of the processes.

The abdominal portion is composed of five segments, the last bearing the furca. In females the furca is distinctly to be seen, each furcal branch along its outer edge being covered with a fringe of leaf-like bristles (fig. 7).

Most characteristic of the form is the conical process on the anterior edge of the inferior ventral side of the fifth abdominal segment, this process serving as support of the reflected hind part of the abdomen. Moreover in females the S curve of the body is due to the circumstance that the dorsal faces of the

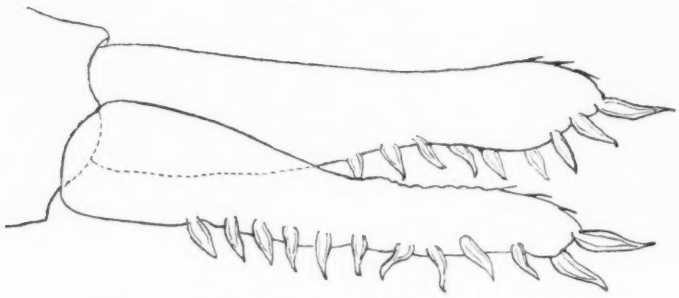

Fig. 7. Furca of the female. Magnif. about 174 ×.

last thoracic and the first two abdominal segments as compared to their ventral surface are of a considerably greater length, whereas in the third and fourth abdominal segments the relations are reversed. The body of the female being thus orientated it closes the opening leading into the brood pouch and prevents the larvae from falling out of the pouch.

The body of the male also consists of 16 segments and the repartition of the segments is the same as in the female. But in the male the segmentation on the whole is of a more primitive character and besides they lack of a number of those secondary modifications which are connected with the care of the young (fig. 8).

The cephalic portion bears only the shearslike antennules and the oral pyramid with three pairs of appendages—the mandibles and the maxillulae and maxillae. All the mouth appendages are enclosed in the upper lip.

The thoracic portion contains six segments and bears six pairs of natatory limbs. Of these the third and fourth pair are truly biramous. Stephensen (1935, p. 7, figs. 4 and 5) however describes in males only 5 or even 4 thoracic limbs. Though the material at my disposal was sufficiently abundant, still I never have observed so strong a variability in the number of thoracopodia—always six pairs of them were present.

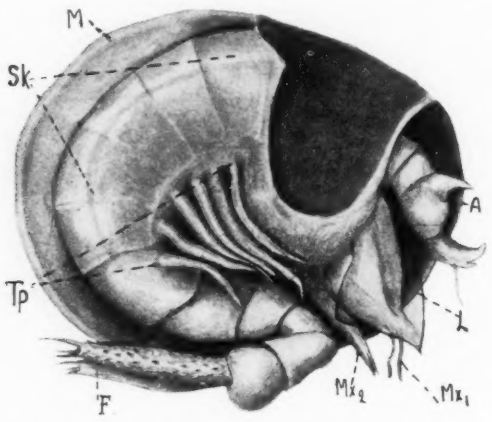


Fig. 8. Male Ascothorax with the left mantle valve removed. Magnif. about 60 ×. *L*—labrum; $Mx_1$—maxillulae; $Mx_2$—maxillae; the other lettering as in fig. 6.

The abdominal portion includes five segments and the terminal segment bears a well developed furca. Adaptive changes being absent in males, the abdomen may be variously orient-

ated. The first abdominal segment bears on its ventral side a small conical process the penis, its length amounts to about half the breadth of the first abdominal segment (fig. 19, p. 187). Both furcal branches bear at their apex three well developed spines respectively. Of these the dorsal is the longest, while the two ventral spines are shorter. The branches are covered all over with very small spines (figs. 5 and 8).

The number of the abdominal segments indicated by DJAKONOV (1914) is quite exact; there are five segments plus the furca. STEPHENSEN (1935, pp. 6—8, fig. 5) is of opinion that in males the abdomen is composed of four segments. No similar observations could be made on my material in which f i v e abdominal segments were always to be found.

VOL. 27 1946

### e. The cephalic appendages.

#### 1. *The antennules.*

The antennules are shear-like, and are composed of five joints—my observations in this respect agree entirely with STEPHENSEN's findings (1935, pp. 5 and 6, fig. 3). According to DJAKONOV (1914) they possess six joints. The antennules of females and males differ somewhat in their structure.

In t h e f e m a l e s they have the aspect of a mighty grasping organ (fig. 9a). The first—basal—joint is of an irregulary quadrangular shape. It is much more large than long. At the dorsal edge the chitin is thickened. The anterior edge runs obliquely producing no sharp angles with the dorsal and the ventral edges.

The large s e c o n d joint is irregularly pentagonal. Its fore end is rounded and posteriorly it is immovably jointed with the first joint. Chitinous thickenings are present all along the dorsal edge as well as in the posterior portion of the ventral edge. The third joint, as compared to the first two, is considerably slighter and is nearly triangular in shape. Its extensive dorsal edge is constituted of thick chitin. It is movably articulated with the second joint and its posterior portion is capable of retraction into the second. The *fourth* joint is immovably articulated with the third; it is of a quaint shape. Its dorsal margin forms a protruding process; the process is dentiform and it is split at its end receiving, between the branches of the bifurcation, the pointed portion of the very mobile fifth joint. Behind the bifurcated dentiform process two jointed spines disposed on small protrusions are to be observed. The concave portion of the anterior edge, as well as the double dentiform process are covered with thick chitin and so is the ventral edge.

*The fifth* joint presents the aspect of a hook curving upward. It is very movably articulated with the fourth joint. On its dorsal (inner) side the joint is smooth and bears no additional structures. It is covered all over with thick chitin, the chitin extending onto the ventral side which bears three additional

Fig. 9. The antennules *a*—in ♀, *b*—in ♂. Magnif. about 52 ×. *Ap 1, 2, 3*—Additional structures belonging to the V joint, $R_{1,2}$—rudimentary muscle in the I joint; $R_{IV}$—rudimentary muscle in the IV joint; $fl_V$—flexor muscle of the V joint; $ext.V_{1,2,3}$—extensor muscles of the V joint; $fl.III_{1,2,3}$—flexor muscles of the III joint; $ext.III_{1,2,3}$—extensor muscles of the III joint; $Ext_{1,2}$—extensor muscles of the anterior portion of the antennule; *FL*—flexor muscles of the anterior portion of the antennule; $Fl.A_{1,2}$—flexor (raising) muscles of the antennule; $Ext.A_{1,2}$—extensor (lowering) muscles of the antennule.

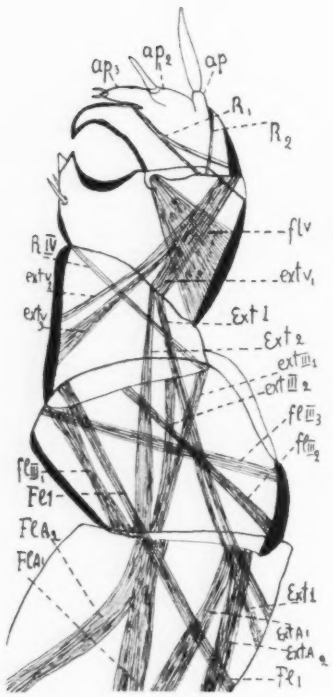


Fig. 9b.

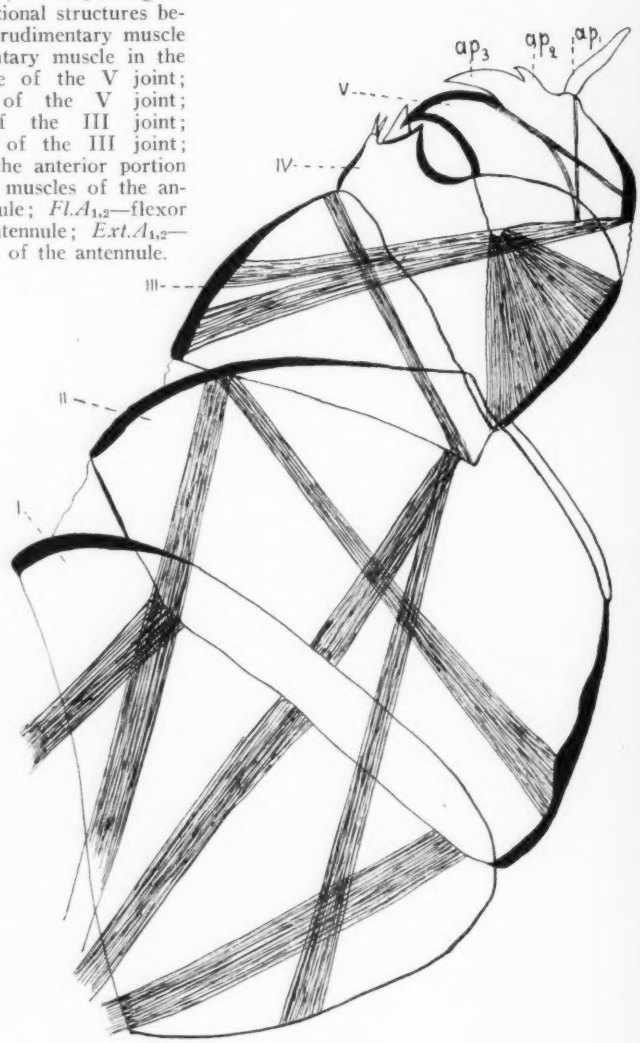


Fig. 9a.

structures; one long articulated spine and two nonarticulated lobules which STEPHENSEN (1915, fig. 3 a) erroneously considers to be jointed.

The antennules of males are much more slender than those of the females, though they are relatively much more developed. The difference consists in that the first two joints are somewhat slighter, they are about as long as they are broad (fig. 9 b). The fourth and fifth joints are similar to those of the femals, only the fifth joint is more strongly armed although the number and location of the additional structures are the same as in the female.

—*The musculature of the antennules.* It is strongly developed and is disposed in a very characteristic way. We shall begin with the description of the musculature in the fifth (apical) joint, as this order of description may help to a clearer understanding of the functioning of the muscles. The fifth joint possesses two rudimentary muscular strands. One of these runs from the basis of the jointed bristle and attaches at the middle of the hind edge of the joint. The other strand arises anteriorly to the fore lobe of the fifth joint and runs towards its lower posterior angle (fig. 9 b, $R_1$ and $R_2$). About its middle this strand separates in two unequal strands the larger one attaching behind the finer strand.

It is to be concluded, from the fact that the muscles of the fifth joint are rudimentary, that in the course of evolution this joint was formed by fusion with at least one anterior joint.

The fourth joint comprises the musculature which serves to put the fifth joint into motion. Some of these muscles extend further and attach in the third joint. The muscle adductor of the fifth joint is attached to its upper angle, the joint forming here a hook-like apodem. The other end of this muscle attaches to the ventral edge of the IV joint and takes up nearly the whole surface (fig. 9 b, *F.I.V*). The extensor muscle of the V segment is much less strong. It is attached to the chitinous ridge of the hind inferior angle of the V joint. In the IV joint this muscle separates into three strands and the largest of these attaches to the posterior edge of the IV joint low down in the last third of the joint, while the two other strands run further and attach in the third joint to the chitionous ridge of its upper edge (fig. 9 b, *Ext.*$V_1$, *2, 3*).

From the border line between the third and fourth joints arise three muscular strands. 1) Diagonally all along the joint runs the rudimentary adductor muscle of the IV joint (fig. 9 b, *R.IV*). From the absence of an antagonist to this muscle it might be inferred that the articulation between the second and third joints is on its way to disappearance. The two other strands arise from the lower third part of this articulation and are attached: the upper strand—to the hind edge of the second joint, the other—to the middle of the inferior edge of the first joint. These two muscles act as flexors of the three anterior antennular joints (fig. 9 b, *Ext.1* and *2*). An abundant musculature is to be found at the border line between the third and second joints. From the upper posterior angle of the III joint arise three flexor muscles of the third joint together with the whole anterior end of the antennule. One of these muscles runs towards the border line between the first and second joints (*Fl.III*), the other is attached to the lower posterior angle of the first joint (*Fl.I*), the third, having crossed the second joint is attached to the fore end of the chitinous ridge at its ventral edge (*Fl.III, 2*). Two flexor muscles of the III joint arise from the interior hind edge of the third joint and attache together at the upper third of the hind edge of the II joint (*Ext.III, 2*). At the border line between

the first and second joints arises the principal musculature which has the command of the movements of the antennules as a whole. Two flexor muscles are attached to the upper third of the articulation (fig. 9 b, *Fl.Ant.1* and *2*). The extensors—of which there is also two—arise from the lower third part of the articulation (fig. 9 b, *Ext.Ant.1* and *2*). No special musculature is to be found in the first joint as it is joined to the second segment by a nearly unmovable articulation. The opposite ends of the muscles have the command of the movements of the antennules, they are attached to the dorsal part of the head on both sides of the mantle suture. The musculature of the antennules is the same in females as in males, so that there is no need of discussing it separately.

On the whole it may be concluded that the antennulae are composed of two portions which differ functionally. The anterior portion consists of the coalescing III and IV joints together with the movable articulated V joint. The latter acts as dactilus, while the rôle of pleon belongs to the bifid dent-like process of the IV joint. This shearslike portion is a grasping organ; it is of the type of the *Chela*. The second portion which serves as basis to the first is represented by the considerably less movably jointed first and second joints. The antennule as a whole is movably articulated with the cephalic portion.

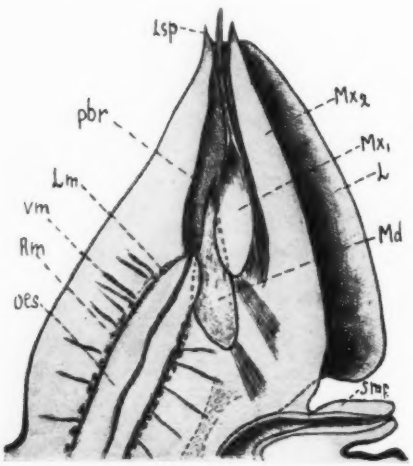


Fig. 10. Oral pyramid in sagittal section (graphic reconstruction). Magnif. 95 ×. *L*—labrum; *Md*—mandibles; *Mx*$_1$—maxillulae; *Mx*$_2$—Maxillae; *np*—opening of the excretory duct; *smp*—submaxillary papilla; *Oes*—oesophagus; *Lm*—longitudinal muscle of the oesophagus; *Rm*—circular muscle; *Vm*—dilatator muscle of the oesophagus; *pbr*—prebuccal cavity; *Lap*—dent on the labrum.

*2. The oral pyramid.*

In the head, behind the antennules lies a trihedric oral pyramid, or as some authors name it the oral cone. This organ, in Ascothorax ophioctenis being trihedric it in noway answers to the designation of "cone" and for this reason the designation "oral pyramid" seemed to me to be more apposite.

As mentioned above the formation of the pyramid is due to the increase in size of the upper lip, which serves as sheath to the three pairs of piercing and sucking appendages. At its basis the oral pyramid is somewhat constricted. The orientation of its sides is such that one of them is directed forward while the other two look backwards. Behind, the edges of the upper lip are free and lie at a certain distance from each other (fig. 10), the protrud-

ing anterior edge is elongated in a sharp chitinous dent-like process.

The *mandibles* are small and pointed; when at rest they do not protrude beyond the sheath (fig. 11). The *maxillules* (*maxillae I*) are typical sucking appendages. They are constituted of a broad basal portion, about half as long as the pyramid, and of a very long and narrow anterior end elongated in a groove-like chord which is about one and a half time as long as the basal portion and protrudes far beyond the edge of the sheath (fig. 12). These groove-like elongated ends are of prime importance in the sucking process. Joined together they form a tube and it is through this tube that the food is sucked in.

Fig. 11. Mandibles. Magnif. about 210 ×.

Fig. 12. Maxillula. Magnif. about 210 ×.

The *Maxillae* (*maxillae II*) are represented by a well developed unpaired organ. They are somewhat longer than the sheath and their ends protrude in the form of two pointed spines (fig. 13). Primarily the maxillae appear as a paired organ but on the animal reaching the imago stage they fuse together. The coalescence occurs along their inner edges, nearly all along the appendages, the distal ends of the maxillae alone remaining free. The line of fusion is characterised by a suture consisting of a groove and two bolster-like thickenings running along the edge (fig. 13).

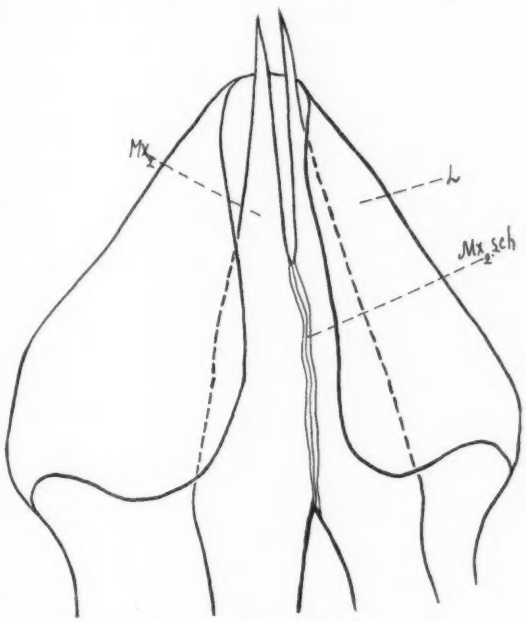


Fig. 13. Maxillae and the posterior edges of the labrum. Magnif. about 240 × $Mx_2$—maxillae; *sch*—suture between the maxillae; *L*—labrum.

STEPHENSEN (1935, fig. 3) described in the Ascothorax ophioctenis female an unpaired oral appendage but in males he found no such *central organ*.

However no such organ was found by me in Ascothorax ophioctenis, although this point was specially investigated. Neither by boiling in KOH, nor by reconstruc-

tion based on serial sections could positive results be obtained. STEPHENSEN's description gives no clear idea neither of the nature of this organ nor of its origin.

### f. The appendages of the thoracic portion.

In the females the thoracic limbs are leaf shaped, they are adapted to the sustaining of a current of water in the mantle cavity. The change of water is needed for the respiration of the embryos in the brood pouch. Moreover these appendages possess in part the function of gills; this is to be inferred from their structure as abundant lacunes are contained in them (fig. 1, plate II).

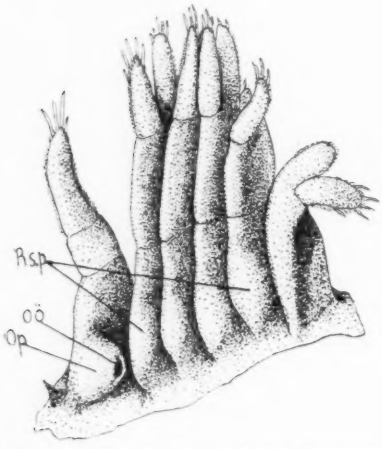


Fig. 14. General view of the thoracic limbs. Magnif. about 77 ×. *Oö*—opening of the oviduct; *Op*—papilla of the oviduct; *R.S.P.*—Localisation of the receptacula seminis.

The first pair is uniramous; it is constituted of three joints: a protopodite consisting of two joints and a rudimentary exopodite with from 5 to 6 bristles at its end (fig. 15[1]). In the outward basal angle of the coxopodite lies a papilla bearing the opening of the oviduct (fig. 14). In the papers of DJAKONOV (1914) and of STEPHENSEN (1935) the first pair of the thoracic appendages is given the character of a nonsegmented conical appendage.

The second and the fifth pair are very similar in structure. They are bifid and are composed of a protopodite consisting of two joints and joined to the protopodite—of an exo- and an endopodite, both respectively consisting of but one joint. They are unmovable and seem to have coalesced with the protopodite. The endopodites bear long bristles and fine setae which are most numerous in the fifth pair.

The third and fourth pair are likewise biramous and are equally very much alike. They possess a protopodite constituted of two joints and of an exo- and endopodite—both consisting of two joints and bearing setae and bristles at their ends. The protopodite has several long setae (fig. 15, *III/IV*). Similarly to what has been found for the second and the fifth pair in the outward basal angle of the protopodite of the third and the fourth pair lie the receptacula seminis (fig. 15, *i.s.*).

The sixth pair is not fully biramous, the endopodite coalescing with the protopodite. The reduction however has not gone so far as to permit to consider these appendages as uniramous. In all instances a fairly long vestigial endopodite was to be found. The exopodite is composed of one joint and is

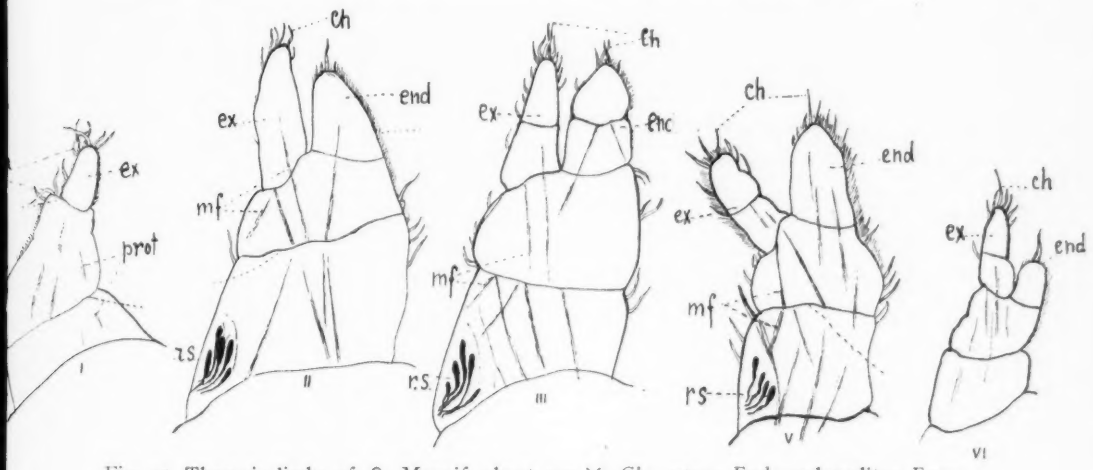


Fig. 15. Thoracic limbs of ♀. Magnif. about 100 ×. *Ch*—setae; *End*—endopodite; *Ex*—exopodite; *mf*—muscular strands; *Prot*—protopodite; *rs*—receptacula seminis; I—IV sequence numbers of the thoracic limbs.

movably articulated with the protopodite. The endopodite is covered with fine setae, the exopodite bears long bristles besides being, like the endopodite, covered with fine setae. The sixth pair bears no receptacula seminis.

This sixth pair of appendages was described by DJAKONOV (1914) and by STEPHENSEN (1935), both authors erroneously considering them to be uniramous.

*In the males* the thoracic limbs have in many cases lost their biramous nature though they still retain their character as swimming appendages.

*The first pair* is composed of two joints, it is uniramous. The apical joint bears a seta at its end. It is difficult to decide about the homology of these two joints, they are probably protopodite joints, while of the exopodite the terminal seta alone persists (fig. 16, *I*).

*The second and fifth pair* are very like in structure. They have a protopodite, composed of two joints a reduced exopodite and an endopodite constituted of one joint bearing apically three long bristles (fig. 16, *II* and *V*).

*The third and fourth pair* are biramous but the endopodite is fused with the two jointed protopodits. The exopodites are well developed they are movable and bear apically three long setae respectively (fig. 16, *III* and *IV*).

*The sixth pair* is uniramous, it is constituted of a twojointed pro-

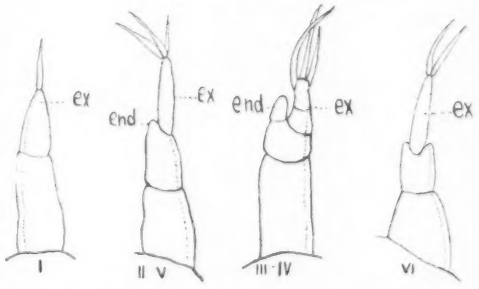


Fig. 16. Thoracic limbs of the male. Magnif. 52 ×. Lettering as in fig. 15.

topodite and a movable exopodite represented by one segment bearing apically two long bristles (fig. 16, *VI*).

Consequently my findings differ strongly from STEPHENSEN's description (1935, pp. 6—8, figs. 4—5) in which this author erroneously indicates that in males the thoracic limbs are non articulated and uniramous.

In conclusion it is to be noted that in females and in males the reduction of the limbs takes to a certain extent a parallel course. In both cases the reduction proceeds from the *apical to the middle part* of the limb. The first and the sixth pair are the first to undergo reduction, next come the second and the fifth while both in females as in males the third and fourth pair of limbs are the least reduced and their typical structure is more conspicuous.

## B. THE INTERNAL ANATOMY.

### a. The integument.

The integument in Ascothorax ophioctenis is represented by a chitinous layer and the underlying hypoderm. The chitin covering the body of the animal is not of equal thickness. It is thicker in the exterior parts and thinner in the parts turned inside. It is thinnest in the articulations as well as in the apical portions of the ducts of the reproductive and the excretory systems, the oesophagus and the hind gut. The chitin is thicker in all the places where muscles are attached as well as at the ends of the antennules (IV and V joint), at the end of the upper lip and the three pairs of oral appendages. On the branches of the furca also the chitin is thicker as compared with the covering of the abdominal segments.

The chitin is slightly stratified; on applying the Mallory stain an outer, intensely staining, and an inner more feebly tinctured layer may be distinguished. Such a stratification may be found only at the points where the chitin is of considerable thickness. In the thin chitinous cover no stratification has been found. Further, the antennules possess an external layer which takes on a red or orange colour when stained by Mallory.

No *dermal glands* were found in Ascothorax ophioctenis. Neither has a sculpture been observed on the face of the mantle valves—the valves are quite smooth.

### b. The nervous system and organs of sense.

The exceedingly concentrated nervous system of Ascothorax ophioctenis consists of a cerebral ganglion, circum-oesophageal commissures, a sub-oesophageal ganglion, an abdominal amassement and the peripherical system.



VOL
27
194

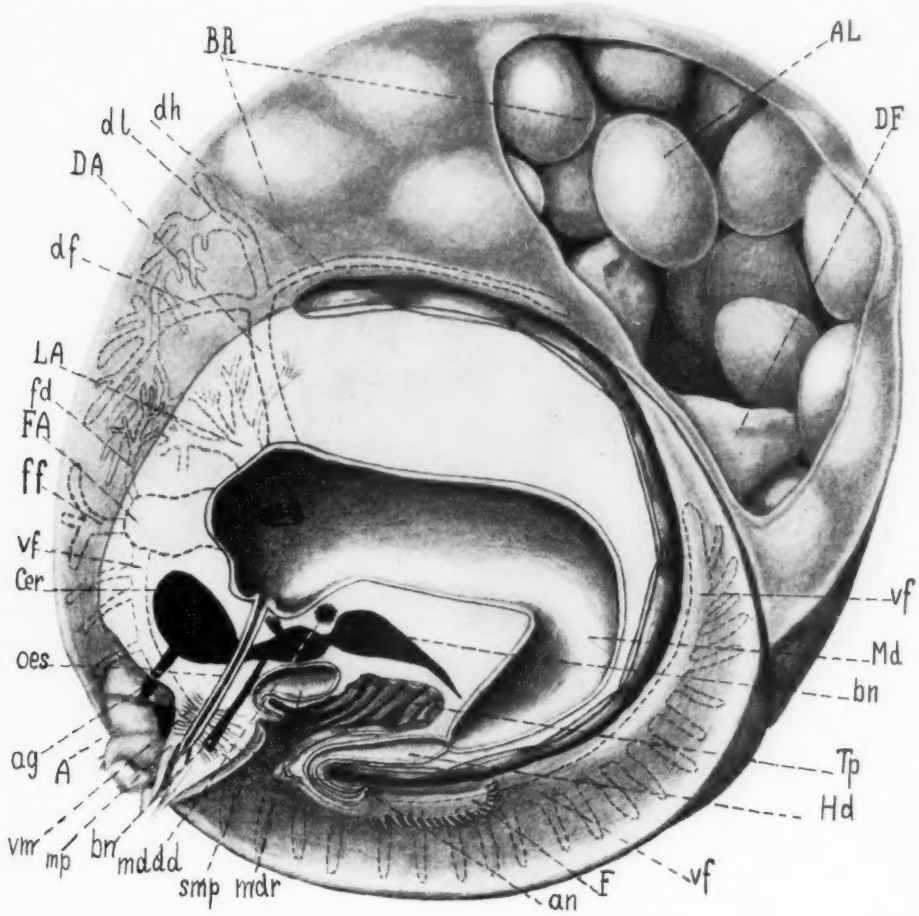


Fig. 17. Ascothorax in sagittal section—graphic reconstruction. Magnif. 32 ×. *A*—antennules; *ag*—antennular ganglion; *AL*—larvae, in the ascothoracid stage; *an*—anus; *bm*—ventral nervous accumulation; *bn*—buccal nerve; *BK*—brood pouch; *cer*—cerebral ganglion; *DA*—dorsal gut diverticulum; *df*—dorso-anterior branch; *dl*—dorso-lateral branch; *dh*—dorso-posterior branch; *DF*—dorsal diverticula in the thoracic region; *F*—furca; *F*—frontal gut diverticulum; *fd*—dorsal branches; *ff*—anterior frontal branch; *Vf*—ventro-frontal branch; *Hd*—hind-gut; *Md*—midgut; *madd*—adductor muscle of valves; *mdr*—maxillary gland; *mp*—oral pyramid; *oes*—oesophagus; *smp*—submaxillary papilla; *Tp*—thoracopodia; *Vm*—dilatator muscles of the oesophagus.

In the males the nervous system shows a somewhat stronger development than in the females—but with these also the concentration has gone so far that the ganglionary composition of the abdominal mass is quite indistinct.

The cerebral ganglion is composed of two ganglionary masses connected by a commissure. About the fibrous substance of the ganglion lies a thick layer of nerve cells forming the main part of the cerebral ganglion. The cerebral

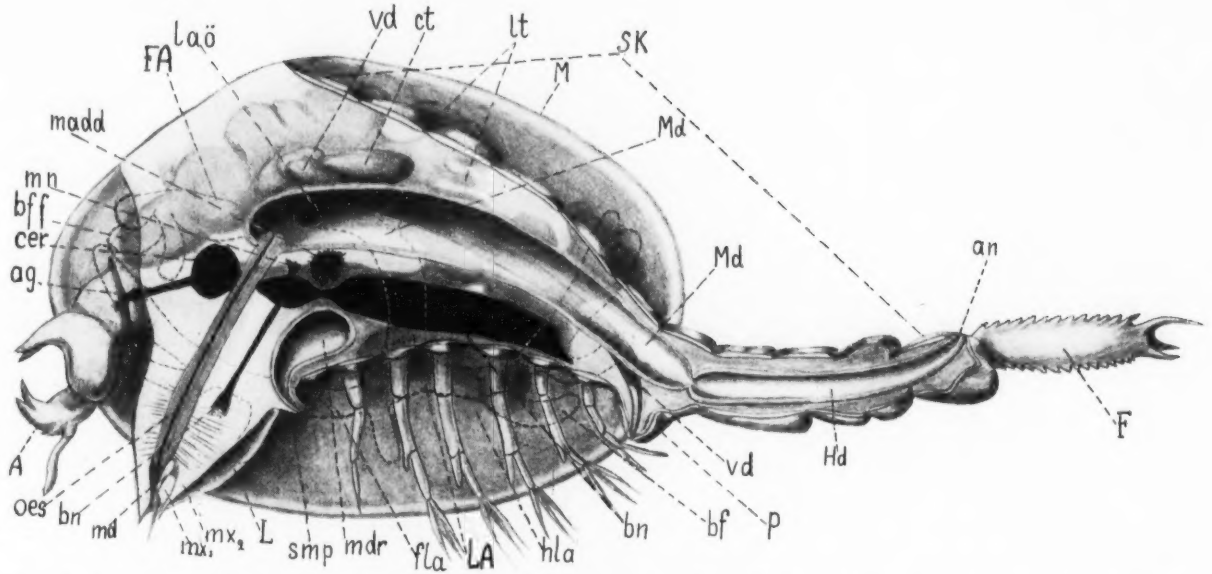


Fig. 18. Ascothorax in sagittal section—diagrammatic reconstruction. Magnif. about 50 ×. *A*—antennule; *ag*—antennular ganglion; *an*—anus; *bf*—branch of a gut diverticulum; *b*—ending blindly; *bff*—branches of the anterior gastric diverticula ending blindly; *Vm*—abdominal nervous mass; *bn*—buccal nerve; *cer*—cerebral ganglion; *ct*—central testicle; *F*—furca; *FA*—frontal gut diverticulum; *fla*—anterior branch of lateral gut diverticulum; *Hd*—hind-gut; *hla*—hind branch of the lateral diverticulum; *L*—labrum; *LA*—lateral gut diverticulum in the mantle; *laö*—aperture of the lateral gut diverticulum; *lt*—lateral testicular lobes in the mantle; *M*—mantle; *madd*—adductor muscle of the valves; *Md*—mid-gut; *mdr*—maxillary glands; *md*—mandibles; *Mx*—maxillulae; *mx-Mx*$_2$—maxillae; *mn*—mantle nerve; *Oes*—oesophagus; *P*—penis; *Sk*—segmented body; *smp*—submaxillary papilla; *vd*—vas deferens.



VOL
27
194

ganglion sends outwards and downwards a pair of strong *antennular* nerves forming *antennular* ganglia in the first joint of each antennule. From each antennular ganglion arises a nervous bundle which in the second antennular joint separates into single fibres. It has not been possible to trace these fibres in their entire course—up to the nervous terminations. Posteriorly the cerebral ganglion sends out the circum-oesophageal commissures—these are short and thick; below the oesophagus they fuse to a suboesophageal ganglion. This ganglion is separated from the abdominal mass by a constriction lying below the adductor muscle of the valves. The *abdominal mass* which is very compact shows no repartition in ganglia. Along the abdominal amassement the fibrous mass shows two swellings and—then goes over into the terminal nerve which tapers away protruding beyond the cellular sheath, which latter likewise tapers away (figs. 17 and 18). The swellings mentioned above represent not separate ganglia but groups of fused ganglia. The suboesophageal ganglion sends out lateral nerves—the mantle and the buccal nerves. *The mantle nerves* arise from the anterior portion of the suboesphageal ganglion and penetrate more or less far into the thickness of the valves, separating there into a number of fine fibres. These nerves are more strongly developed in the females than in the males and the fact is to be put in connection with the strong growth of the mantle valves in them. Below and forward of he suboesophageal ganglion arises a pair of strong buccal nerves which penetrate into the oral pyramid. No nerves supplying the thoracic appendages could be discovered.

In regard of the *histological structure* the data obtained coincide with the description given by KNIPOWITSCH (1892), LE ROI (1907) and PYEFINCH (1936) of Dendrogaster astericola, Dendrogaster (Myriocladus) arborescens and Baccalaureus hexapus respectively. The ganglion cells are of two types: 1) cells with small nuclei and granular protoplasm, the granules staining well with anilin-blue and picro-indigo-carmine. The nuclei are rich in chromatin. 2) Larger cells enclosing larger nuclei which are poor in chromatin. The protoplasm is less granulated and is stained less intensely with anilin blue, taking on a light blue colour. The neuroglia is composed of rather small cells, it envelopes the ganglionary masses as well as the fibrous substance of the nerves.

*Special organs of sense are absent.* Only various setae and bristles are found on the antennules and the furcal branches. The pointed dental protrusions on the anterior end of the labrum are probably to be considered as tactile organs. No eyes.

### c. The gut.

In Ascothorax ophioctenis, as in all Entomostraca four portions of the alimentary system may be distinguished: the fore-, mid- and hind-gut and the gut diverticula; these being exceedingly developed in our form.

1. The intestinal tube begins with *a prebuccal cavity* lying within the oral pyramid (figs. 17, 18). Three pairs of mouth appendages lie free in this cavity from which begins the oesophagus somewhat to the fore of the mandibles. Its tapering end protrudes somewhat into this cavity, the inside of which is lined with chitin. The same is the case in the *oesophagus,* the chitin ending by a free edge on the outer surface of the terminal swelling of the oesophagus within the mid gut. In the oesophagus the chitin reposes on a layer of hypodermal cells with large nuclei; and beyond it lie two layers of muscles. Adhering to the hypoderm lies the layer of longitudinal muscles; its fibres are not quite parallel but run at a certain angle to the longitudinal axis of the oesophagus (fig. 1, plate I). The external layer is composed of circular muscles. It is not continuous but is composed of separate strands which hoop-like encircle the oesophagus. Aside these: in the region of the oral pyramid dilatator muscles are present. Their one end is attached to the oesophagus, the other—to the wall of the oral pyramid (fig. 10, *Vm*). Beyond the oral pyramid no dilatator muscles are to be found—the oesophagus possesses only a longitudinal and a circular musculature. This repartition of the musculature makes it possible for A. ophioctenis to suck in liquid food.

The end of the oesophagus which opens into the mid gut bears a bulbous swelling, it is the so called caput of the oesophagus; it protrudes into the lumen of the mid-gut. The caput is bereft of muscles; it is composed of high hypodermal cells, compressed at their base (fig. 1, plate II).

2. In *the mid-gut* two portions may be distinguished—the central portion running along the whole length of the thorax and the lateral gut diverticula; of these the females possess three pairs which show a very complicated branching; the males have two pairs of such diverticula—their branching is simple. In the females the intricate structure of the gut diverticula is connected with the complicated structure of the mantle and the intestine has retained its typical mode of branching.

The central part of the mid-gut runs all along the thoracic portion; in the second abdominal segment it joins the hind-gut. At the place of connection a constriction is formed.

3. *The gut diverticula differing* in their topography in females and in males—the corresponding descriptions will be given separately.

*In females* (fig. 17), owing to the development of the brood pouch, the massive parts of the mantle valves are shifted forward. This causes peculiar changes in the topography of the gut diverticula; the females possess three pairs of diverticula—a frontal, a lateral and a dorsal—one (after GIESBRECHT'S (1913) terminology).

The frontal diverticula arises from the anterior portion of the mid-gut which strongly protrudes in a forward direction. This protrusion may be considered



VOL
27
194

as an unpaired basal portion of the frontal diverticulum (fig. 17, *F.A*). Each of these ducts divides in three branches bearing blindly ending prolongations.

The dorsal branch curves dorsad along the anterior margin of the mantle (fig. 17). The short frontal branch extends towards the anterior ends of the valves (fig. 17, *f.da*). The largest of all is the ventral branch—it takes a downward direction and runs all along the inferior thickening of the mantle (fig. 17, *Fva*). This branch gives off in its course numerous ramifications ending blindly; they enfold in a thick net the ascending and the descending branches of the ovaries.

The lateral protrusions arise from the mid-gut somewhat behind the level of the caput of the oesophagus. They penetrate into the right and left mantle valves at the level of the mid-gut and very soon divide into three or four secondary branches; these branches in their turn give off ramifications and blind prolongations localised in the middle portions of the mantle (fig. 17, *Lat*).

At about the same level a pair of dorsal prolongations arise from the dorsal wall of the mid-gut (fig. 17, *DA*). They run upwards as far as the region of the fusion of the valves and then curve backwards. At the point of reflection three branches take their beginning: a short frontal branch running along the anterior end of the body so that it comes to meet the branches of the frontal diverticulum (fig. 17, *df*). Another branch runs along the mantle suture and continues along the dorsal margin of the mantle where it very soon ends blindly. This branch gives off no prolongations (fig. 17, *dh*).

The third branch takes its course towards the antero superior portions of the elevated portion of the valves. It is fairly strongly developed and ramifies to a considerable extent (fig. 17, *dl*).

In males the topography of the gut diverticula is much more simple. They are represented by only two pairs—a frontal and a lateral pair. From the frontal wall of the mid gut arise two short frontal diverticula (fig. 18, *fa*)—one on each side. Here they ramify producing 3 to 4 blindly ending ducts.

The second pair arises from the lateral walls of the mid-gut, somewhat behind the level of the caput of the oesophagus. The diverticula take their course towards the mantle valves. First they run for a short space in a backward direction they lie at the level of the mid-gut. On penetrating into the valves, they turn sharply downwards, separating in the lower third of the valves into an anterior and a posterior branch (fig. 18, *fla* and *hla*). These branches run parallel to the lower edge of the valves. Each of the branches gives off three blind diverticula directed towards the lower margin of the valves.

4. *The histological structure of the mid-gut.* It is the same in its central portions as in the lateral diverticula. Its walls are lined with two sorts of cells: slightly vacuolized cuboidal cells and other of a higher shape with strongly vacuolized protoplasm at their distal ends (fig. 2, plate I). Most cells are nearly regularly

cuboidal—their protoplasm is granulated and slightly vacuolized. The distal ends of such cells are composed of a rather dense protoplasm staining intensely. Their large nuclei lie nearer to the basal end of the cell, they are rich in chromatin and contain distinctly staining nucleoli.

In the basal portion of the high cells the protoplasm has a granulated structure and contains vacuoles which lie far apart. The distal portion is strongly vacuolized and presents the aspect of a spumous knob. The nuclei lie in the basal portion; their structure is similar to that of the nuclei in the low cells.

It is difficult to establish the nature of the high cells, but presumably these are older cells originated from the low ones by excrescence of the distal ends filled with vacuoles. The contents of the vacuoles stain well with anilin blue, and when iron hemotoxylin is used they take on a greyisch tone which, on appliance of eosine, changes into brown; when lichtgrün is employed their colour is greyish green.

With their proximal ends the cells of the intestinal epithelium repose on a basal membrane produced by the connective tissue envelope of the intestine. This tissue is crossed by thinly scattered muscular fibres forming a network

VOL
27
194

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PLATE I.

1. Oesophagus, longitudinal section. Magnif. 650 ×. Heidenhain's hematoxylin. *Hyp*—hypoderm cells; *l.k.*—longitudinal muscles; *R.m.*—circular muscles; *Oes.lum.*—lumen in the oesophagus.

2. Wall of the mid-gut, longitudinal section. Magnif. as above, Mallory. *bg.*—connective tissue; *Bm.*—basal membrane; *k*—nucleus; *P.sch*—plasmatic layer; *vac*—vacuoles; *Lz*—elongated cells; *Rm*—circular muscles; *Lm*—longitudinal muscles.

3. Problematic (unknown) glandular organ in ♀; a part of the organ. Magnif. 450 ×. Mallory. *k*—nucleus; *n*—nucleolus; *fgr*—granula staining with fuchsine; *gr*—granula staining with Anilin blue; *ap*—external plasm; *ip*—internal plasm.

4. Wall of the maxillary gland and body wall. Magnif. 450 ×. Mallory. *lac*—lacune; *Ch*—chitin; *Hyp*—hypoderm; *bg*—connective tissue; *m*—muscular fibre; *m.dr.wd*—wall of the maxillary gland.

5. Wall of the brood pouch. Magnif. 450 ×. Mallory. *a.Ch.*—external chitin; *ich*—chitin of the inner wall; *Hyp*—hypoderm; *bz*—blood cells; *Qm*—transverse (constrictor) muscles; *Lm*—longitudinal-muscles; *Lac*—lacunes.

6. Spermia from the receptacula seminis. Magnif. 850 ×. Heidenhain's hematoxylin.

7. Hind-gut, cross section. Magnif. 864 ×. Mallory. *Bs*—"Bürstensaum" layer; *ch*—chitin.

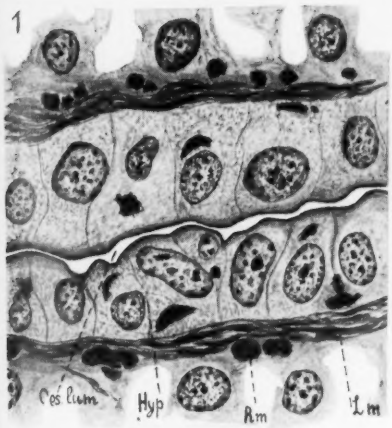
8. Vas deferens, longitudinal section. Magnif. 450 ×. Borax carmine. *sp*—spermia; *bgk*—nuclei in connective tissue cells; *vd.wd*—wall of the vas deferens; the arrow points in the antero—posterior direction.

9. An oocyte in section. Magnif. 450 ×. Borax carmine. *Dot*—yolk; *Kbl*—nucleus.

10. Ovary in section. Magnif. 450 ×. Heidenhain's hematoxylin. *ov.wd*—wall of the ovary.

11. Ripe oocyte. Magnif. 450 ×. Borax carmine. *Dot*—yolk grains; *Kbl*—nucleus; *Ovd.wd*—oviduct walls.

12. Receptacula seminis in the thoracopodia in ♀; in oblique and cross section. Magnif. 450 ×. Heidenhain's haematoxylin. *ch*—chitin; *bgz*—connective tissue cells; *rs*—receptacula seminis; *rs.wd*—wall of the receptacula seminis; *Hyp.z*—hypoderm cells; *bg*—connective tissue.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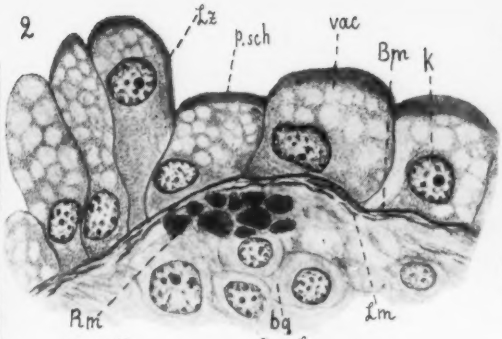
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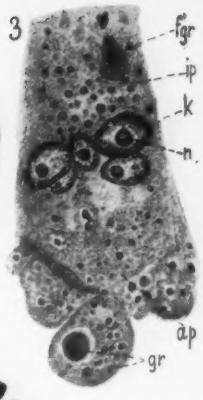
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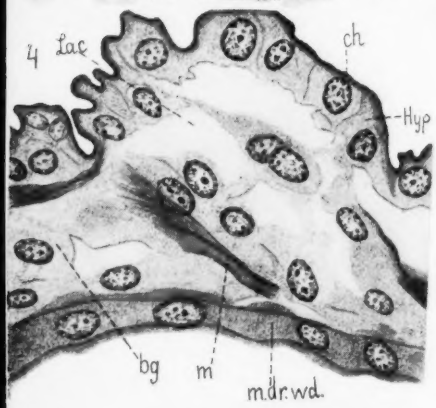
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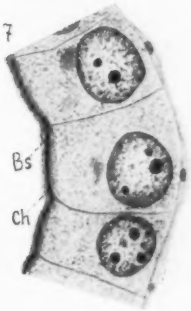
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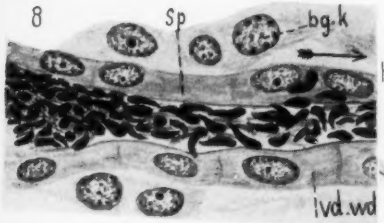
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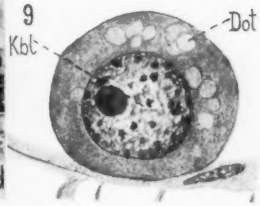
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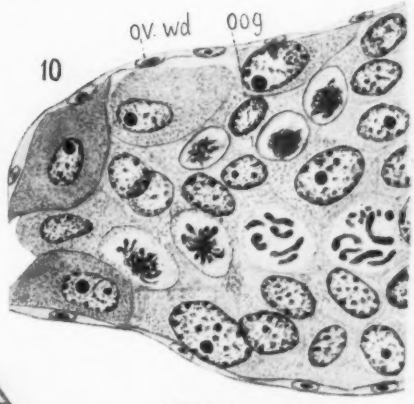
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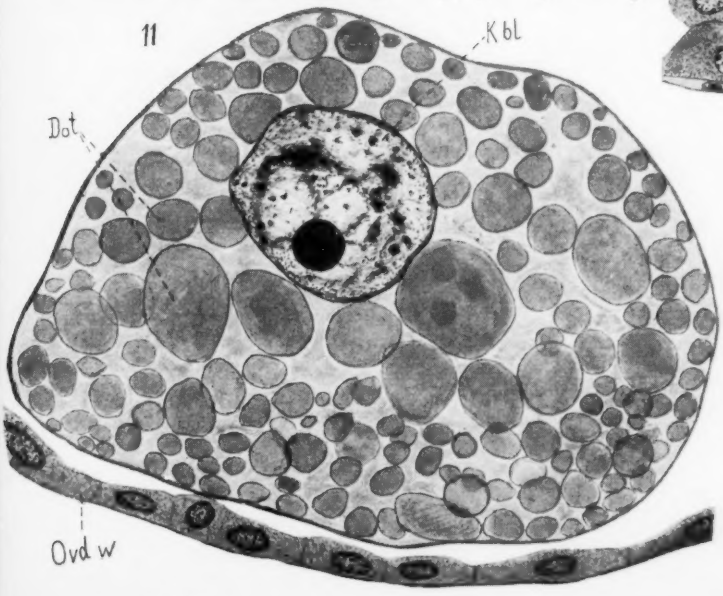
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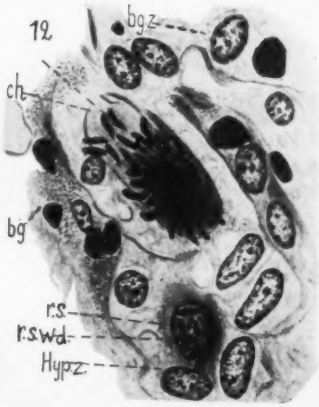
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about the mid-gut. These fibres run in an oblique direction and intersect with each other.

*The histological structure* of the gut diverticula including their blind ends is fully similar to that of the mid-gut; the only difference consists in that their muscular layer is less developed.

5. *The hind-gut* begins at the constriction located in the second abdominal segment; it is the boundary between mid- and hind-gut. The hind-gut is represented by a tube tapering towards the hind end; its outwards opening —the anus lies between the branches of the furca. On its inside the mid-gut is lined with chitin which, at the outer border of the anal opening, goes over into the chitinous covering of the body (fig. 7, plate I). The chitin reposes upon a hypodermal layer of which the main part of the wall of the hind-gut is composed. The hind-gut possesses furthermore an envelope of connective tissue in which no muscular fibres could be found.

The hind-gut has a like structure in females as in males.

VOL 27 194

### d. The muscles of the body proper.

This chapter is dedicated mainly to the analysis of the musculature of the body proper, its main modifications, and further the musculature of the body proper, its main modifications, and further the musculature which has the governing of the movements of the thoracic limbs. The musculature of the antennules and the mantle has been described above.

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PLATE II.

1. Segmented portion of the body ♀, in sagittal section. Magnif. 40 ×. Mallory. *DA*—dorsal branch of the gut diverticula; *Lac*—lacunes; *Fdf*—dorsal prolongation of the frontal branch; *FA*—frontal branch; *Fvf*—ventral prolongation of the frontal branch; *Cer*—cervical ganglion; *ÖK*—the caput of the oesophagus; *A*—antennule; *Bkn*—buccal-nerve; *Oes*—oesophagus; *mdr*—maxillary gland; *Smp*—submaxillary papilla; *bn*—abdominal nerve; *F*—furca; *An*—anus; *Hd*—hind-gut; *Md*—mid-gut; *m*—muscle; *Tp*—thoracopodia; *Ovd*—oviduct; *M*—mantle; *Dhf*—dorso-posterior gut diverticulum; *Ov*—ovary.

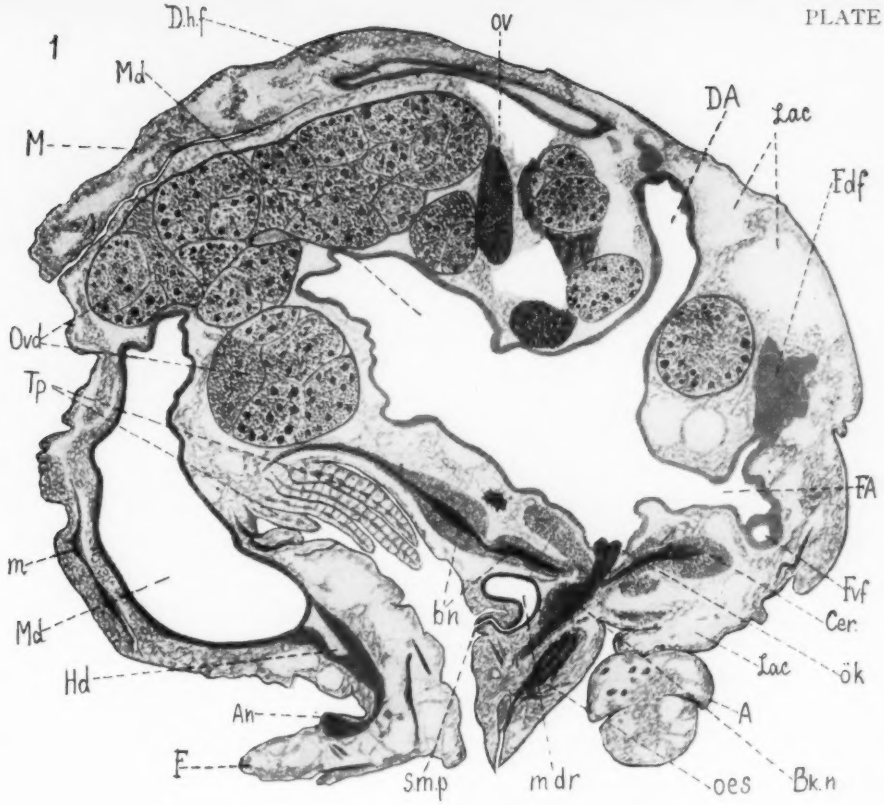
2. Point of attachment of the antennules to the wall of the bursal cavity in section. Magnif. 190 ×. Borax carmine. *A*—terminal joint of the antennules; *Bw*—bursal wall.

3. Point of penetration of the oral apparatus into the wall of the bursal cavity—in section. Magnif. 190 ×. Borax carmine. $Mx_1$ and $Mx_2$—maxillulae and maxillae; *Bw*—bursal wall.

4. Infested bursa (frontal section). Magnif. 19 ×. Borax carmine. ♂—male; *D*—gut of the female; *Bik*—brood pouch; *Lrv*—larvae; *Bw*—bursal wall; *ovd*—oviduct; *n*—abdominal ventral nerve; *m.add*—adductor muscle; *mdr*—maxillary glands; *A*—antennules; *Bö*—bursal aperture.

5. Testis lobes and vas deferens in cross section. Magnif. 190 ×. Borax carmine. *ltest*—left testes; *ve*—vas efferens; *Vd*—vas deferens; *c test*—central testes; *rst*—maturation stages; *spt*—spermatids; *sp*—spermia; *spc*—spermatocytes.

6. Problematic glandular organs in ♀—in cross section. Magnif. 190 ×. Mallory. *söggl*—supraoesophageal ganglion; *udr*—problematic glandular organ; *ovd*—oviduct with ova; *Kw*—body wall; *A*—antennule.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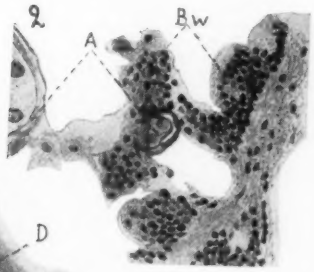
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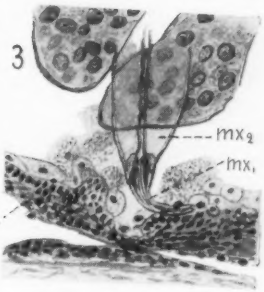
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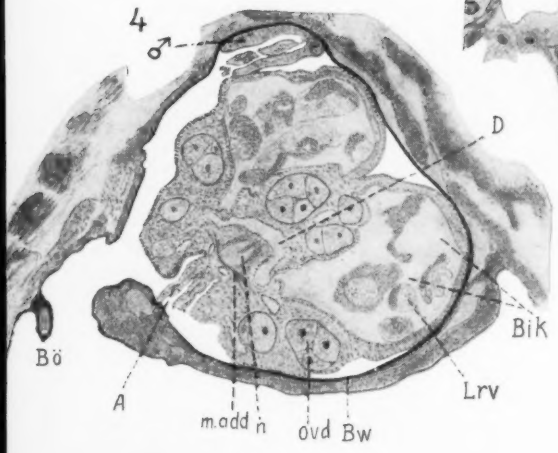
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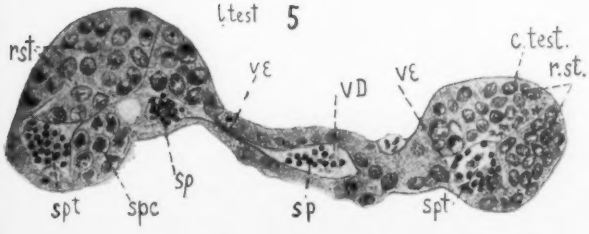
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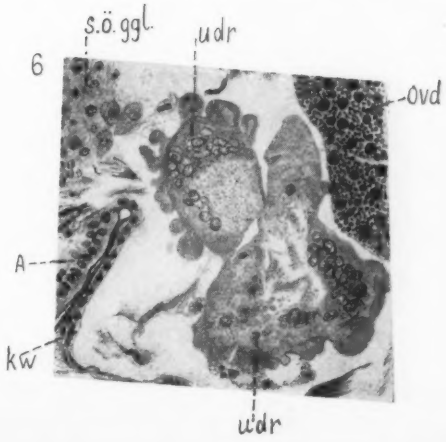
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*The musculature of the body proper is according* to type; it is composed of flexors lying ventrally and of extensors localised dorsally. These, the most important muscles, of the body are—in males—very distinct (fig. 19). The picture presented by the females is somewhat different. A part of the muscles of the body have grown rudimentary, such are: the ventral muscles of the thorax and the abdomen, the dorsal muscles of the abdomen and partly of the thorax. Certain muscles have modified their function. Out of the muscles of the dorsal portion of the thorax a strong musculature of the dorsal gut diverticula came to be formed. The muscles of the last abdominal segment are changed into motor muscles of the furcal branches (fig. 19).

Of the special muscles—of great importance is the adductor muscle of the valves. This muscle is strongly developed in males while in females it is much less conspicuous. The musculus adductor scutorum (*s.M.digastricus*) lies between the intestine and the nervous system at the point where the nervous system presents a constriction localised between the suboesophageal ganglion and the abdominal mass. Its bundles run perpendicularly to the outward walls of the mantle valves. Above the constriction lies a muscle which, beginning as a compact strand, spreads in a cone and attaches to the walls of the mantle valves. This muscle is originated from the musculature belonging to the last cephalic (maxillary) segment.

Moreover, in the head and the thoracic portion lie the motor muscles of the limbs governing the movements of the limbs. These are the adductors and abductors of the antennulae, next the much feebler muscles of the oral appendages and the appendages of the thoracic portion (fig. 19). They are very homogeneous in their structure. Adductor and abductor strands are disposed in each segment in the following way. In the adductors the one end is attached to the anterior dorsal edge of the corresponding segment while the other end is attached to the base of the limb. In the abductors one end is attached to the posterior margin and the other to the base of the limb (fig. 19).

The musculature of the thoracopodia is feebly developed and it appears frequently to be rudimentary. It is best developed in such instances in which the endo- and the exopodite have retained their mobility. In such cases the flexor and extensor muscles of the limb's branches may be observed.

The muscle fibres are attached to the body wall or to the organs on special protuberances produced by the hypoderm and the connective tissue. In some cases chitinous prolongations—apodems protrude into the body cavity. Such is the case in the V joints of the antennules. The adductor muscle of valves forms a large attaching surface. Here the chitin of the mantle is thickened. A correlative thickening of the chitin may likewise be observed at some other points of attachement of muscles. The thickeness of the surface of attachment is proportionate to the thickeness of the muscles attaching to it.



VOL 27 194

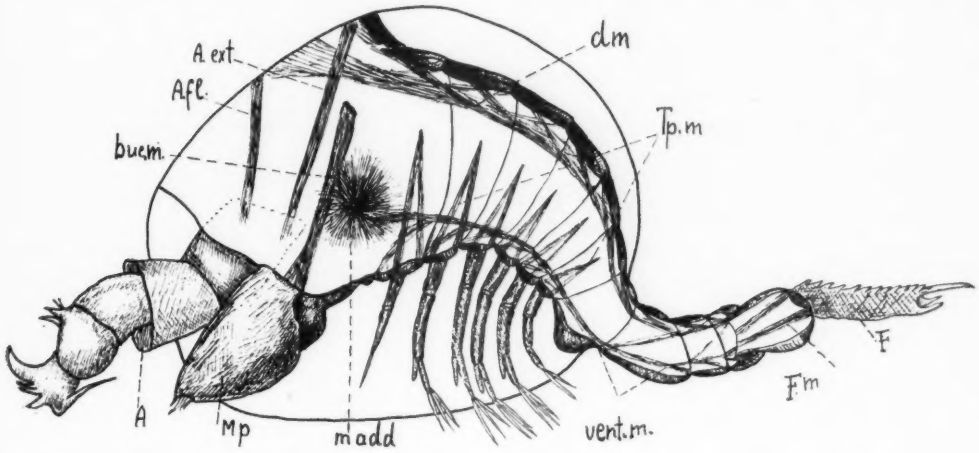


Fig. 19. Diagram of the localisation of the main muscles of the body (combined from sections and in toto preparations). Magnif. about 46 ×. *A*—antennule; *Aext*—lowering muscle of the antennule; *Afl*—raising muscle of the antennule; *bucm*—buccal muscular strand; *dm*—dorsal muscles of the segments; *F*—furca; *Fm*—muscles of the furca; *Mp*—oral pyramid; *madd*—adductor muscle of the valves; *Tpm*—motor muscles of the thoracic limbs; *ventm*—ventral segmentary musculature.

It has been possible to obtain distinct evidence as regards most muscles that they are striped. The striped character is indistinct only in the muscles surrounding the vesicle of the excretory system, and in the fibres about the oesophagus and the intestine.

The location of the musculature, especially in the limbs is exceedingly stabile. It has been found to persist in rudimentary segments; it is frequently even if the articulation has disappeared (v. the description of the V antennular joint in the adult and in the Ascothoracid larva). In view of this there can be no two opinions as to the importance of the location of the musculature appendages. Also it is no less important as a systematical feature which, together with certain other peculiaritis, may help in the systematical determination of the Arthropoda. We insist here especially upon this circumstance, so as to again attract to this fact the attention of the systematists who frequently do not take sufficient notice of these so very important morphological characters.

### e. The connective tissue.

The connective tissue represented by a loose mass containing large cavities (lacunes) fills all the space between the inner organs and the body wall. It is composed af separate cells, or groups of cells connected with each other by prolongations more or less extended. It produces the tunica externa of the gut, of the maxillary gland and of the ducts of the reproduction system. At

the points of attachment of the musculature the connective tissue forms islet-like amassements. In the cavities and in the space between the connective tissue cells circulates the blood.

### f. The lacunary system.

The lacunary system takes here the place of the vascular system which is absent.

The lacunes form a system of variously dimensioned cavities about and between the inner organs. Within the antennules, the oral pyramid, and the thoracic appendages a system of lacunes is likewise present—it is connected with the lacunary system of the body proper. The lacunes are distributed irregularly. They are most numerous about the intestine and the germinative glands—both in the body proper as in the massive portion of the mantle valves. In the wall of the brood pouch a thick network of lacunes is included (fig. 1, plate II). The larger lacunes belong to the body proper, they lie between the intestine and the ventral wall of the body, in its thoracic and abdominal portions.

The cavital fluid—the lymph—which fills the lacunes contains lymphocytes of various size. They are numerous about the intestine, near the gut diverticula, and the reservoir of the maxillary glands. Equally numerous are the lymphocytes in the lacunes of the wall of the brood pouch and those of the thoracopodia.

### g. The excretory system.

There is one pair of typical maxillary glands; they lie ventrally, between the sub-oesopageal ganglion and the body wall. Each gland is composed of two parts: a large sac-like blindly ending reservoir and a duct by means of which this reservoir opens outwards (fig. 16, 17 and 18, *Mxdr*). The cavity of the vesicle is considered to be a vestige of the coelom—some authors for this reason designate the reservoirs of the maxillary glands as coelom. The ducts of the maxillary glands are homologous with the nephridial ducts. In respect of their histological structure the two parts of the organs differ. The cavity of the reservoir is lined with flat epithelium cells possessing rather large oval shaped nuclei—their long axis is parallel to the cells' surface. The nuclei are not especially rich in chromatin and a nucleolus is distinctly visible. In the plasma of the cell granular inclusions of various size may be observed—these may be are excretory producte (?). The inclusions stain well with iron hematoxylin—taking on a black tint. When anilin blue is employed they are light blue and the substance sedimented on the face of the cells turned towards the cavity of the reservoir stains in the same way. The epithelial cells repose on a thin layer of connective tissue which is composed of supporting



VOL
27
194

cells. Lymphocytes with granular protoplasm were found closely adhering to the reservoir wall (fig. 4, plate I). A thick network of large and small lacunes envelopes the reservoir of the maxillary glands. In the lacunes numerous lymphocytes are contained. At the point in which the—reservoir goes over into the efferent duct the cells grow higher; and those which form the lining of the duct are cuboidal. The nuclei of the cells in the efferent duct are relatively small and their plasma contains no granules. The lumen of the duct is large at its beginning, but it grows narrower towards its opening, and in its distal portion within the maxillary papilla is scarcely visible (fig. 10, *Np*). It has all along a chitinous lining.

### h. The reproductive system.

Ascothorax ophioctenis is dioecious; the form possesses a distinct sexual dimorphism.

1. *The reproductive system of the male* is composed of testes localised in the mantle valves, of their ducts, opening into the vasa deferentia, and of a small conical penis lying in the first abdominal segment; the v. deferentia open outward at its apical end (fig. 18).

*The testes* are represented by a single unpaired gland lying above the proximal portion of the mid-gut. To the right and to the left into the mantle valves extend more or less developed testicular lobes. They are rounded, irregularly shaped and are mainly localised in the dorsal and the middle portion of the valves (fig. 18).

At the point where the testes penetrate into the mantle valves they lie most closely to the dorsal margin of the valves.

When strongly developed, the testes descend in separate lobes as far as the inferior margin of the valves.

Each glandular lobe is composed of distinct areas containing spermid at different stages of development (fig. 5, plate II). The peripherical areas contain spermatogonia, while in the deeper areas more advanced maturation stages as well as spermatids may be observed.

In the areas situated at the very base of the lobe, the vas efferens begins, here lie also the portions of the testes containing spermatids and ripe spermia, which likewise fill the vasa efferentia.

The vasa efferentia fuse into larger ducts opening into the *vasa deferentia*; these begin in the cephalic region above the mid-gut somewhat anteriorly to the level of the adductor muscle of the valves. The vasa deferentia run along the whole of the thoracic region. In its first half they lie laterally along the dorsal side of the gut and posteriorly they go over to the ventral side. In the first abdominal segment they turn sharply downwards and open into the conical penis, which lies on the ventral side of the segment. The penis is of

relatively small size, its length amounting in length to half the width of the first abdominal segment. The walls of the vasa efferentia are formed on the one hand by the follicles of the testes, and on the other—by a thin membrane lined on its inside by one layer of law epithelial cells.

The walls of the vasa deferentia consist of an inner layer constituted of similar low cells, and a tunica externa formed of connective tissue which envelopes the ducts on the outside.

The terminal ends of the v. deferentia are on their inside lined with chitin reflected from the surface of the penis. The penis, like the body, has a chitinous covering; inside it is filled with connective tissue.

2. *The reproductive system of the female* is represented by an unpaired ovary lying dorsally of the gut. Its lateral prolongations extend into the mantle. These prolongations run upwards through the segmented body towards the fore part of the valves. They have a sinuous course and penetrate into the thickened portion of the ventral edge of the mantle where they run in a loop entering posteriorly into the massive part of the valves and further into the hind portion of the thorax. Within the thorax they run in loops above the gut. On reaching the border of the abdomen they go over onto the ventral side, run in a forward direction and open outwards. These paired openings lie on special conical papillae at the hind surface of the first thoracic appendage. The division zone lies in the unpaired portion of the ovary while in its lateral portions maturation stages may be observed. Further on the ovaries go gradually over into the oviducts. Within the oviducts the egg cells are enriched with yolk. The egg cells in the oviducts contain a various amount of yolk; we find there from young eggs cells deprived of yolk and up to ripe ova fully laden with yolk. In the ripe egg the distribution of the yolk is such that the smaller grains lie peripherally, and the larger ones—near the nucleus (fig. 2, plate I). The size of the ripe eggs is of from 0.20 to 0.25 mm. The wall of the oviducts is composed of one layer of flat epithelial cells and a thin tunica externa of connective tissue. The chitin which covers the first pair of the thoracic appendages is reflected inside into the terminal portion of the oviducts so that this portion has a chitinous lining on its inside.

3. *The receptacula seminis* (testes—according to LACAZE-DUTHIERS and PYEFINCH, dermal glands—according to KNIPOWITSCH) in Ascothorax ophioctenis are of a very peculiar character. They lie in the outward basal angles of the protopodites of the II to V pair of thoracic limbs (figs. 15 and 14). Each appendage bears at the basal part of the protopodite from 9 to 18 club-shaped chitinous pouches—their granular contents staining well with nuclear stains (fig. 12, plate I).

Evidence was obtained by comparative observations that in respect of shape and staining capacity certain inclusions present the same aspect as the spermia found in the v. deferentia. The chitinous lining of the receptacula seminis



VOL
27
194

could be recognised by its characteristic glitter and by its capacity to obtain a blue colouring when stained with anilin blue. The chitin reposes on a hypodermal layer composed of cuboidal cells. The space between the receptacula seminis is filled with connective tissue. As mentioned above, in the thoracic limbs—at the place of localisation of the receptacula seminis — a swelling arises. In female individuals of various age the receptacula seminis were found filled with spermia.

### i. An unknown glandular organ in females.

In the Ascothorax ophioctenis females a large paired syncytial organ of glandular nature is found lying in the fore part of the mantle valves (fig. 6, plate II). The organ is irregularly lobed and lies on both sides of the suboesophageal ganglion; the inner lobes of the organ reach as far as the ganglion with which they come in contact in its posterior part, behind the buccal nerves and somewhat anteriorly of the mantle nerves. Here the ganglionary and neuroglial tissue give off several prolongations which penetrate into the mantle valves and interlace there with the inner lobes of the glandular organ. This organ lies in the inner part of the valve, it never coalesces with the integument, and never even extends so far; it is surrounded by lacunes and by the branches of the gastric diverticula, while below it lie the branches of the ovary. No ducts were discovered to this organ.

The "gland" is enrobed in a plasmatic membrane in which no separate cells can be distinguished. The numerous nuclei lying below this membrane adher closely to each other. They are considerably smaller than those of the hypoderm and do not exceed in size the connective tissue nuclei.

The central part of the organ is taken up by a cavity which is filled with a granular product of secretion. This substance stains with plasmatic stains (anilin blue, eosin etc.). In the plasmatic portion of the organ a similar granular substance is contained but there is less of it (fig. 3, plate I).

The gland—its tissues presenting the above mentioned peculiarities—differs most distinctly from the other organs. It has never been found to possess any other envelope save the plasmatic membrane. *No such "glands"* were found either in *males* or in the *Ascothoracid larvae* although they were most assidiously sought for.

It was first surmised that these glands represent rudimentary cement glands, but soon we had to abandon this hypothesie because the cement glands: 1) are modified dermal glands and possess well developed ducts, 2) they attain their highest development not in the adult Cirripedia, but in the cypris stage, 3) they possess a distinct cellular structure (Nussbaum 1890, Krüger 1923, Broch 1927); 4) they are localised in the cephalic portion and not in the mantle valves.

The absence of ducts, of a chitinous lining, the subdermal location and the syncytial character of the gland—all this speak against the possibility of homologising them with the cement glands of the Cirripedia.

KNIPOWITSCH (1892) mentions glandular formations in the anterior portion of the body of Dendrogaster astericola, but the glands described by this author have a cellular structure (see KNIPOWITSCH fig. 37, plate II); there is no likeness between them and the glands we have discovered. Neither is this gland homologous with the gastric glands described by PYEFINCH (1936) in Baccalaureus hexapus, as the gastric glands possess ducts opening in the anterior portion of the mid-gut. The author gives no picture of them.

The glands occurring in other Crustacea may be classified in two types—dermal and subdermal glands. To the first belong various "olfactory", glands, luminous glands, and the frontal organs of unknown function (KÜCKENTHAL and KRUMBACH, Bd. III—"Crustacea"—1927; GIESBRECHT—1913).

To the other type belong the enigmatic subdermal organs in Ostracoda females. MÜLLER, G. W. (1927) found them in Paradoxostoma triste MÜLLER, G. W., in which large glandular cells lie in the mantle valves below the hypoderm.

In parasitic Copepoda—in the genus Brachiella—a Y-formed syncytial organ localised in the anterior portion of the head has been described by CUVIER.[1] This brief survey of the glandular formations in Crustacea indicates that the gland described cannot be considered as a dermal gland but must be put into the group of subdermal formations. However its peculiar structure renders it unlike any of the glands previously described in Crustacea. The function of the "gland" is not clear. Neither do we know with what organs it may be homologised. These questions remain as yet unsolved, in spite of all our efforts to find an answer to them. The only sure fact is that they are not homologous with the cement glands of the Cirripedia.

## C. DEVELOPMENT.

This chapter treats of such data respecting the development of the form described as may be of importance in the analysis of the phylogenetic relations of our group and its systematical position. More detailed data on its embryology and metamorphosis will be given in a special paper.

### a. The fertilization and the laying of the eggs.

The fertilization is external and occurs at the time when the mature ova leaving the oviducts penetrate into one of the brood pouches. In the propulsion

[1] Cited after KÜCKENTHAL & KRUMBACH, Bd. III, N 4.

of the ova the thoracic limbs play an active part. Before it penetrates into the brood pouch the egg must travel backwards along the basis of at least two thoracic limbs. As mentioned above the thoracopodia II to V are the bearers of the receptacula seminis. The ovum in its travel produces pressure on the basal parts of the thoracic limbs, presses out the sperm from the receptacula, and is fertilised by it.

The way covered by the egg penetrating into the mantle cavity lies presumably back of the second pair of the dorsal thoracic elevations which protrude into the brood pouch.

From the ova n a u p l i u s larvae are hatched; these larvae, remain within the pouch and continue their development there untill they reach the ascothoracid stage (see further p. 194).

OL.
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### b. The nauplius.

The nauplius is very characteristic in its aspect. It possesses a very strongly developed carapax rendering it's appearance very uncouth. Below the carapax lies an amassment of embryonic yolk which persists up to the metanauplius stage.

The dorsal carapax possesses soft rounded contours and is bereft of any sort of additional structures or frontal spines so characteristic for the nauplius stages of the Cirripedia. Unpaired eye absent.

The characteristic three pairs of appendages—the uniramous antennules, the biramous antennae and the mandibles—bear natatory spines—these are less strongly developed and also less numerous than in the free swimming nauplius larvae of the Ascothoracida.

The first pair has three spines; the second bears 4 spines on the exopodite and 2 spines on the endopodite. The third—3 on the exopodite and 2 on the endopodite.

STEPHENSEN's (1935) data differ somewhat from mine—see below: table I.

TABLE I.

| | Antennules | Antennae | | Mandibles | |
|---|---|---|---|---|---|
| | | Exopodite | Endopodite | Exopodite | Endopodite |
| As found by STEPHENSEN | 3 | 7 | 2 | 4 | 3 |
| As found by me | 3 | 4 | 2 | 3 | 2 |

The reason of this divergence lies probably in that the larvae examined were of different age, although in my material the larval stages on which my observations were made greatly ressembles the stage reproduced in STEPHENSEN's work.

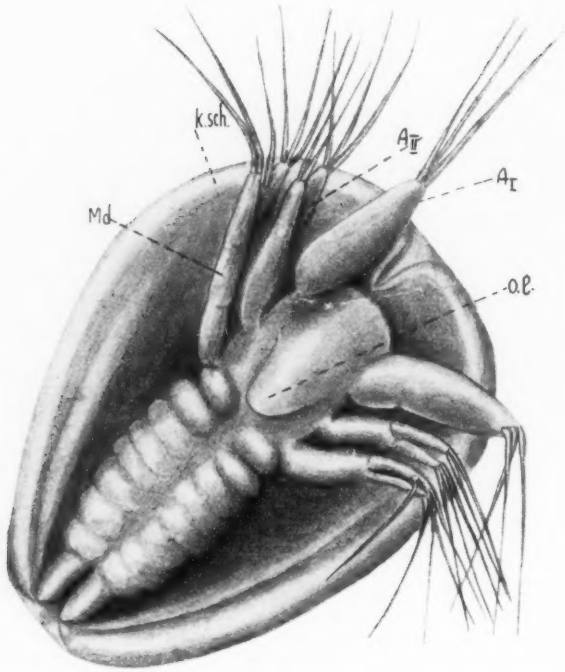



Fig. 20. Metanauplius of Ascothorax viewed from the ventral side. Magnif. about 90 ×. $A_1$—antennules; *A*—antennae; *ksch*—cephalic carapax; *Md*—mandibles; *ol*—labrum.

### c. The metanauplius.

The metanauplius stage is characterized by an increase in size of the carapax below which the primordia of the future valves of the ascothoracid stage are already visible. Also primordia of the thoracic limbs make their appearance (fig. 20). The exact number of moults preceding the subimaginal metamorphosis has not as yet been established.

### d. The ascothoracid stage.

In this stage the larvae have a distinctly segmented body enveloped by a bivalved mantle which is the dorsal carapax of the nauplius stage. Being strongly increased in size the body of the larva is but scarcely covered by these valves. Dorsally they are joined by a short dorsal suture lying in the region of the cephalic portion of the larva; this part of the larva coalesces in its dorsal and lateral regions with the mantle valves (figs. 21 and 22).

The parts of the body and the articulation are the same as in the adult. Size—0.3 to 0.4 mm.

The *cephalic portion* is not segmented; it consists of 5 segments fused together and bearing 4 pairs of appendages—the antennulae and the oral pyra-

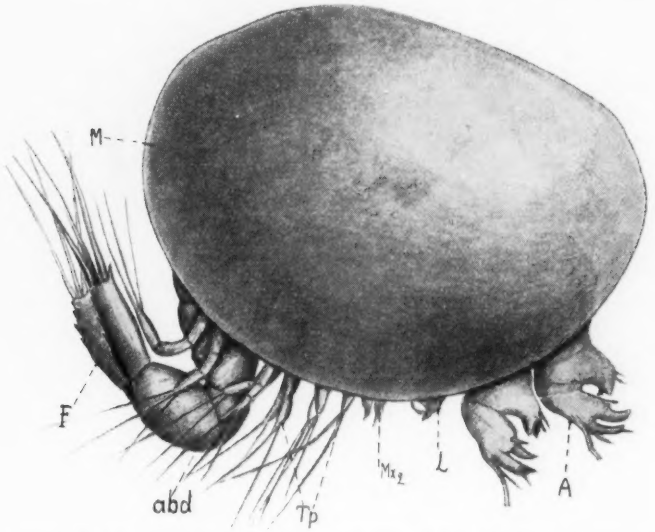



Fig. 21. Larva in the ascothoracid stage. General view. Magnif. about 48 ×. *A*—antennules; *l*—labrum; *Mx*$_2$—maxillae; *abd*—abdomen; *F*—furca; *Tp*—thoracic limbs; *M*—mantel.

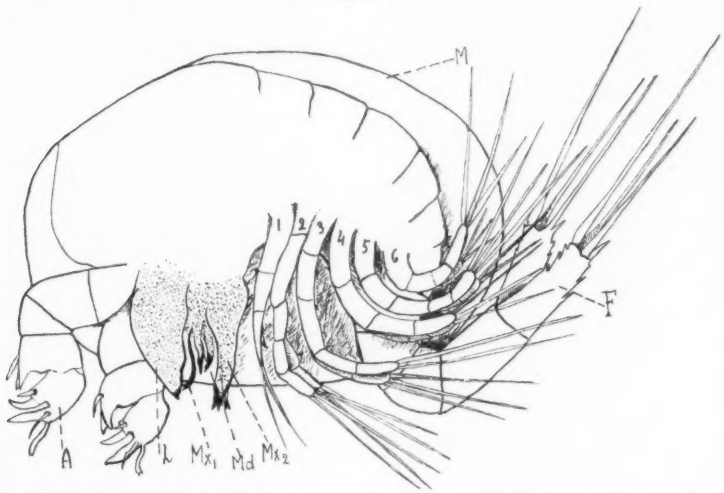



Fig. 22. Segmentation of the larva in its ascothoracid stage. Magnif. 48 ×. *Md*—mandibles; *Mx*$_1$—maxillulae; *1—6* thoracic limbs in the order of their sequence; *M*—mantle; *F*—furca; *A*—antennules.

mid—of the piercing and sucking type—which is composed of three pairs of appendages. Antennae are absent—they disappear at the setting in of the ascothoracid stage.

The *thoracic portion*—is composed of six segments, each of which bears one pair of swimming biramous appendages.

The *abdominal portion*—has five segments; it is mobile and bears at its end a well developed swimming furca, each furcal branch possesses at its end 3 long spines and 1 short one; the dorsal spine being the longest. Distally along the dorsal and the ventral edge of both branches small spines—3 on each side are present. As already mentioned by DJAKONOV (1914) the first abdominal segment bears ventrally a small conical protuberence.

The *antennules* possess 5 joints; they are shears-like but differ from those of the adult Ascothoracida in that they present in their structure numerous primitive characters. The antennules may be described as follows (fig. 23).

The *first joint* is very broad and has a rounded dorsal edge.

The *second* is of an irregular quadrangular shape.

The *third*—is nearly triangular; its dorsal margin is of considerable length. It is movably jointed to the second, and immovably to the fourth joint.

The *fourth* is the largest. It is trapezium shaped. In its antero-dorsal angle it bears a large double dent and on the dorsal margin somewhat behind the dent—two articulated setae.

The *fifth joint* presents the greatest interest. It is of a nearly regular quadrangular shape and possesses no tapering projection that curves upwards. On its distal end it bears a terminal claw possessing a rudimentary articulation represented by a chitinous bolster. Dorsally, behind the claw, the joint gives off a small process which bears two lateral spines, ventrally the joint bears numerous appendages. The articulated spine sits on a broad base which is fused with the base of the hind lobe. Before it lies another anterior lobe; it is very large, equalling the terminal claw in length. Between the anterior lobe and the terminal claw lies a small chitinuous plate which is parallel to the posterior margin of the segment. In their location and partly in respect of their development the additional structures of the fifth joint present a certain likeness with those of the apical (VI) antennular joint in Synagoga mira Norm. (DJAKONOV likewise mentions that the antennulars consist of five joints, but he gives no description of them.)

The *oral pyramid* is very like that of the adult form but it differs from the latter in that its labrum is less developed, the labrum not as yet enveloping all the appendages—and that the maxillae lie behind the posterior edges of the labrum. The appendages are very similar in character to those of the adult, the maxillae presenting the greatest difference—they are as yet but slightly fused together—their pointed distal end is double and not single as in the adult. The maxillulae and the mandibles are largely identical with those of the adult.

The *thoracic limbs* are all biramous swimming appendages. The endopodites are rudimentary in the first and the sixth pair.

The first pair is biramous, it has a well developed exopodite and an exceedingly reduced endopodite. The exopodite bears two terminal spines (fig. 23).



VOL
27
194

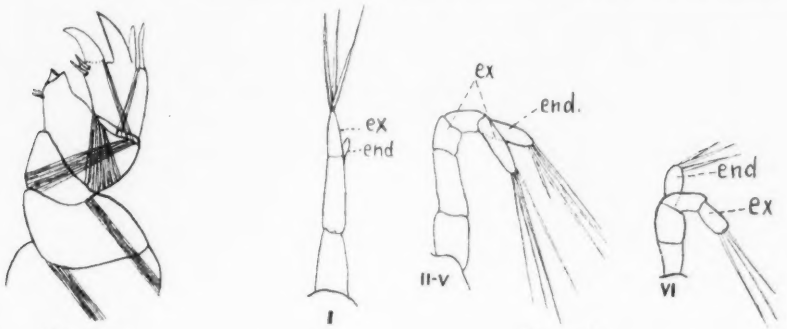



Fig. 23 a. Fig. 23 b.

Fig. 23. Limbs of larva in its ascothoracid stage. Magnif. about 48 ×. *a*—antennules; *b*—thoracic limbs; *end*—endopodite; *ex*—exopodite; *I—VI*—the limbs in the order of their sequence.

According to Djakonov (1914) the first pair is not jointed and is much shorter than all the others.

From the *second to the fifth pair* inclusively all the appendages present the same structure—they are typical natatory limbs and their exo- and endopodites bear swimming spines. The two branches in these limbs are equally well developed. The *sixth* pair is represented by quite typical biramous limbs; it is distinguished from the others by its somewhat smaller size and the unequal development of its branches; the exopodite consists of two joints, the endopodite is represented by one segment.

The *internal anatomy* also is like that of the adult—this is especially observed in the males—the structure of the gut and their nervous system presenting a great ressemblance. The gut diverticula are to a certain extent disposed as in the male. As regards the other organs mention must be made of the presence as in adults of an adductor muscle lying between intestine and nervous system, that is to the ventral side of the gut.

Neither cement glands nor any organs ressembling them are present. In this the Ascothoracid larva differs from the cypris larva. In Cirripedia in which the antennules function as suckers these appendages frequently bear the openings of the cement gland ducts. The cephalic portion in the cypris-larvae is exceedingly well developed at the expense of the development of the cement glands. In connection with this a ventral suture makes its appearance in their mantle, and at the same time the dorsal suture increases considerably in length. Further to be noted is the slight development of the abdomen with its furca and the dorsal—in relation to the gut—localisation of the adductor muscle of the valves.

As may be concluded from this cursory comparison the Ascothorax larvae, and consequently all Ascothoracida larvae differ widely from the Cirripedian cypris larvae to which they correspond. As it presents no ressemblance to any Entomostraca larva it must be considered as a special larval type—the

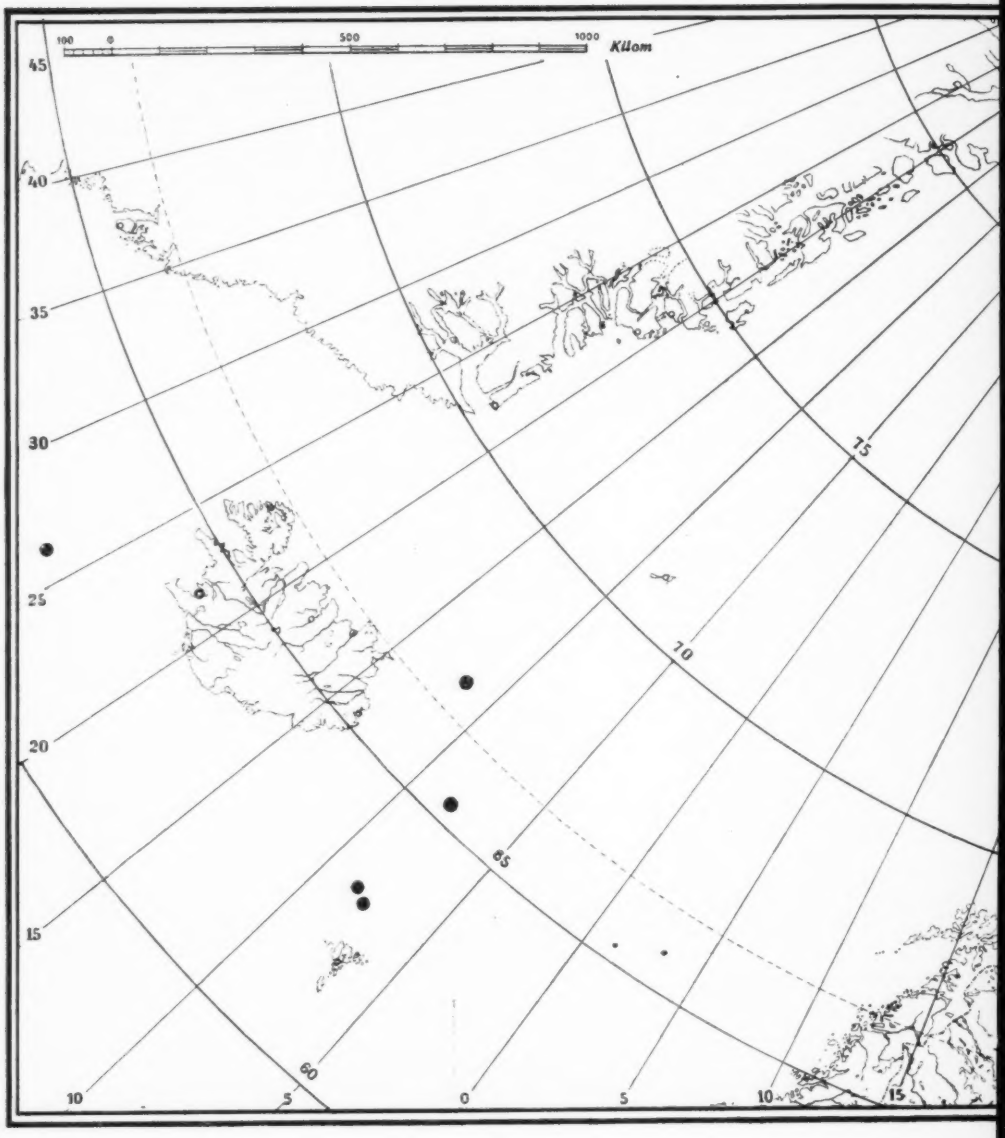
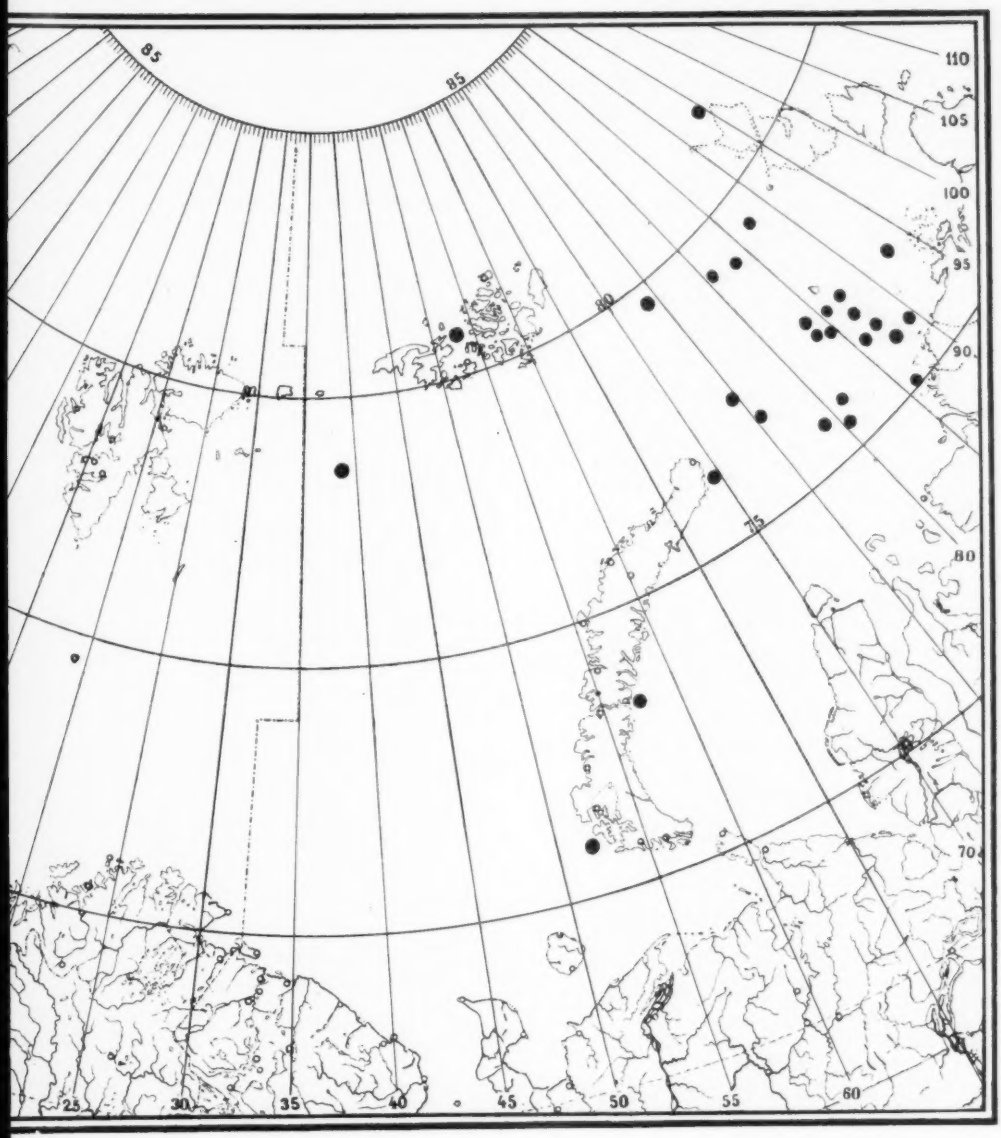



Fig. 24. Chart showin

VOL.
27
1946




istribution of Ascothorax.

*Ascothoracid larva,* just as in Copepoda the corresponding stages are designated as copepodid stages.

The three larval forms here enumerated have that in common that they are respectively very like their adult forms, differing from these in that some organs in them are more feebly developed while the reproductive system has not attained its full development.

This stage agreeing with the adult (imaginal) stages and at the same time sharply differing from the nauplius and metanauplius stages it must be considered not as a typical larval form but as a *subimaginal stage.*

## D. THE RELATION OF PARASITE TO HOST.

a. The distribution of Ascothorax ophioctenis is intimately connected with the distribution of its host—the Ophiuroid—Ophiocten sericeum Forbes (fig. 24), which is widely spread over the area of the Arctic Ocean and the northern region of the Atlantic. Within the areas inhabited by this brittle-star its density of occurrence is frequently very high. In some of the trawl landings from 15 to 20 thousands specimens were secured. Areas in which 2,000—3,000 specimens of Ophiocten sericeum were brought to the surface by the trawl-net are of no rare occurrence off the northern coast of our Union.

Ascothorax ophioctenis occurs less frequently than its host. As a rule it was found in the cases when the specimens of the brittle-star were secured in large numbers.

Ascothorax ophioctenis was first found in the Barents Sea off the Novaja Zemlya coast (L°—71° 10′ N; S°—51° 0′ E), at a depth of 110 m (Djakonov 1914).

By the "Ingolf" Expedition Ascothorax was secured in the Greenland Sea (Stephensen 1935) at the following stations:

S°—61° 44′ N, L°—27° 00′ W, depth 913 m, t° 6.1°, st. 81; 4 oviger.

S°—65° 34′ N, L°—7° 31′ W, depth 1,435 m, t° 0.8°, st. 105; 4 oviger ova and larvae, 1 with male.

S°—66° 44′ N, L°—11° 33′ W, depth 1,571 m, t° 0.7°, st. 110; 4 oviger one of them—with larvae, and 2 with male.

S°—63° 36′ N, L°—7° 30′ W, depth 1,322 m, t° 0.6°, st. 139; 3 oviger, 1 without ova but with male.

S°—63° 22′ N, L°—6° 58′ W, depth 1,278 m, t° 0.6°, st. 141; 1 oviger.

My own collections were made in the North and Central areas of the Kara Sea in 1933 (ice breaker "A. Sibiryakov" at the stations: st. 25, 22 VII, S°—76° 48′ N, L°—93° 40′ E, depth 60 m, 8 infested ophiurids. st. 41, 28 IX, S°—75° 57′ N, L°—87° 01′ E, depth 49 m, 11 ophiurans.

Moreover in 1934 abundant Ascothorax materials were taken by the ice breaker "G. Sedov", see table II:

ZOOL. 27 946



TABLE II.

| Station | Data | Location | | Depth in metres | Bottom | Number of Ophiocten sericeum | Number of infested Ophiuroids | Percentage of infestation |
|---|---|---|---|---|---|---|---|---|
| | | NS° | EL° | | | | | |
| 1 | 27/VII | 76° 50.7′ | 69° 54.5′ | 178 | Grey ooze | 2245 | 4 | 0.18 |
| 12 | 1/VIII | 78° 59.8′ | 80° 27.5′ | 105 | Brown mud | 11(?) | 2 | (?)18.2 |
| 15 | 2/VIII | 79° 00.7′ | 83° 12′ | 115 | Brown mud with sand | 5000 | 5 | 0.10 |
| 17 | 3/VIII | 79° 03.5′ | 85° 48′ | 56 | Brown mud, sand, stones | 3764 | 9 | 0.24 |
| 25 | 17/VIII | 79° 38.6′ | 74° 42′ | 49 | Shelly bottom, grey ooze, sand | 490 | 10 | 2.05 |
| 48 | 3/IX | 77° 29.1′ | 83° 50′ | 57 | Oozy sand together with concretions of ferric magnesia | 8743 | 4 | 0.05 |
| 49 | „ | 77° 10.8′ | 83° 52′ | 56 | Grey ooze with admixture of brown | 482 | 3 | 0.72 |
| 50 | 4/IX | 77° 15.6′ | 85° 30′ | 32 | Oozy sand and gravel | 1839 | 3 | 0.16 |
| 51 | „ | 77° 28′ | 86° 32′ | 112 | Grey ooze with sand | (?)61 | 11 | 18.03(?) |
| 54 | 5/IX | 77° 06.9′ | 88° 40′ | 46 | Brown ooze with admixture of sand | 17000 | 4 | > 0.02 |
| 55 | „ | 76° 53′ | 88° 14′ | 45 | Brown ooze with admixture of sand | 3652 | 1 | 0.03 |
| 57 | 6/IX | 76° 41.2′ | 88° 14′ | 45 | Brown ooze with admixture of sand | 5070 | 11 | 0.22 |
| 63 | 9/IX | 75° 40.6′ | 80° 26′ | 42 | Grey ooze with admixture of sand | 5873 | 22 | 0.37 |
| 64 | 10/IX | 76° 19.8′ | 80° 12.5′ | 46 | Grey green ooze with concretion | (?)20 | 2 | 10 (?) |
| 73 | 19/IX | 76° 02.8′ | 87° 34′ | 42 | Brown ooze together with gravel and boulder stones | 368 | 5 | 1.35 |
| 74 | „ | 76° 02′ | 76° 13′ | 58 | Grey ooze together with sand and concretions | 261 | 4 | 1.11 |
| 83 | 21/IX | 75° 46.4′ | 78° 52.5′ | 58 | Brown mud | 600 | 13 | 0.5 |
| 87 | „ | 76° 30.5′ | 73° 42′ | 98 | Brown mud | 352 | 12 | 3.41 |
| 92 | 23/IX | 76° 17.7′ | 68° 47′ | 97 | Rugged stones, sand, gravel | 1 | 1 | 100 (?) |
| 102 | 27/IX | 73° 09.1′ | 57° 04′ | 112 | Grey sandy ooze together with stones | 5136 | 32 | 0.62 |

Average pr. cent of 0.7°

Judging by the character of its distribution A. ophioctenis may be considered as an arctic form, its occurrence in relation to depth being especially convincing. In the Kara and the Barents Seas this species is found at relatively small depths (from 32 to 178 m). Most illustrative in this respect is its occurrence in the shallow water of the Kara Sea (st. 25 and 41 and 41—1933; st. 17—25 (off the isle of Wise), 48—51, 54, 55, 57, 63, 64, 73, 74 and 83—1934).

On the other hand—in the Greenland Sea A. ophioctenis was found at greater depths (913—1,571 m) and higher temperatures from + 6.1° to + 0.6° (STEPHENSEN 1935). Such a relation to depth is characteristic for all arctic forms belonging to the North Atlantic and has been noticed by various investigators who studied the arctic forms belonging to various groups of the animal reign (GORBUNOV 1934, GURIANOVA 1934, FISCHER 1928, WESENBERG-LUND 1932). There is no need of enumerating the species mentioned by these authors—it suffices to indicate here the characteristic peculiarity common to all these forms—namely occurrence at small depths in the arctic waters and a descent to greater depths in the North Atlantic. This refers also to the Ascothorax host—the Ophiuroid Ophiocten sericeum Forbes.

The Ophiuroid infested with Ascothorax mostly show a swelling of their disk in the interradius disposed at the base of one of the arms. The parasites lie within this swelling—a female and one or more males (3 and sometimes 4 males may be present),—though mostly one male has been observed. Females alone, without males are of exceedingly rare occurrence. In one instance I found, lying in the same bursa, two adult female individuals and one male. The swellings on the ophiuran disk are due to the circumstance that the female Ascothorax ophioctenis has a diameter which considerably exceeds the thickness of the host's disk. Sometimes two, and even three swellings are present—this is the case if the infestation of one specimen of the host is double or triple. In such abundantly infested ophiuroids the disk is considerably deformed. The percentage of infestation is relatively small, on the average it is not above 0.7 %, but occasionnaly it varies from 0.02 % to 3.41 %.

b. *Adult females.* Ascothorax ophioctenis parasitate in the bursal cavities causing a strong distention of the walls of these cavities. The impression produced is that the parasite is enveloped in a cyst. Such a cyst is mentioned by DJAKONOV (1914). But STEPHENSEN's findings, made on dissected specimens, as well as my own observations—on dissected specimens and on sections—have permitted to ascertain that the host produces no special cyst about the parasite, and that the bursal walls alone envelope the parasite. The parasite is immediately enclosed in the bursal cavity which by means of the bursal aperture communicates with the outward world (fig. 4, plate II; fig. 25, 26, 27). The Ophiuroid Ophiomitrella clavigera (Ljungm.) shows a similar reaction, when infested; the bursal cavities of this form are inhabited by a

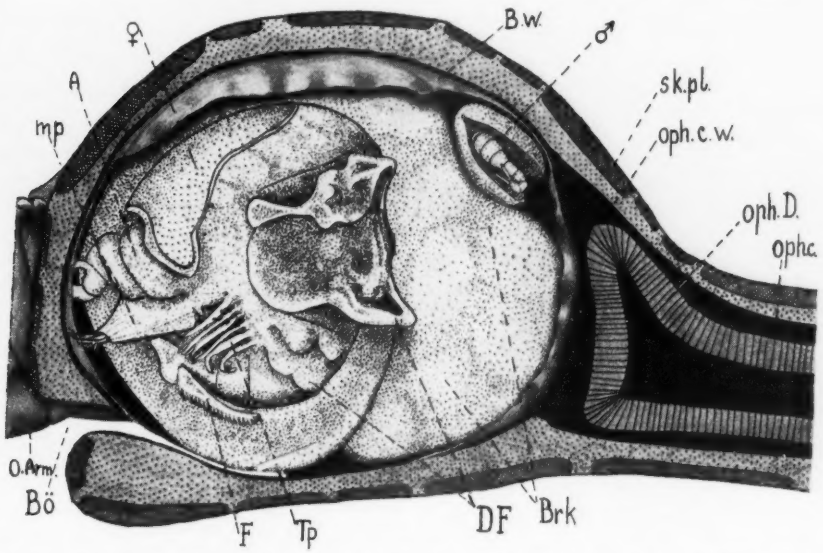



Fig. 25. Diagram of the position of the parasite (and) within the host according to data obtained from section and from dissected hosts. Magnif. 18 ×. *A*—antennules; *Brk*—brood pouch of the parasite; *Bw*—walls of the bursal cavity in the ophiuroid; *Bö*—aperture of the bursal cavity; *DF*—dorsal processes on the thorax of Ascothorax; *F*—furca; *O-Arm*—arms of the Ophiuroid; *Oph.c*—coeloma in the Ophiuroid; *Oph.C.W.*—coelom wall of the Ophiuroid; *Oph-D.*—intestine of the Ophiuroid; *Skpl*—skelettal plates of the Ophiuroid; *mp*—oral pyramid; *Tp*—thoracic limbs of Ascothorax.

parasitic Copepod-Ophiodon appendiculata STEPHENSEN (1935). In other cases the host segregates a close cyst about the parasite. Such a case has been described by FEDOTOV (1915) in Gorgonocephalus eucnemis Müll & Trosch. The host produces dense cysts about Protomyzostomum polynephris FEDOTOV parasitating in its bursae. I found such cysts produced by another species—Gorgonocephales arcticus L. and enveloping the Protomyzostomum sp. which parasitate in its bursae.

The adult female of the parasite does not change its position in the bursal cavity. Its immobility is due on the one hand to the animal being attached to the wall of the bursa by its antennules, and on the other hand it is caused by the pressure of the strongly distended bursal walls. The Ascothorax female is mostly *orientated* in such a way that its mantle opening is turned towards the bursal slit. The fixation of the

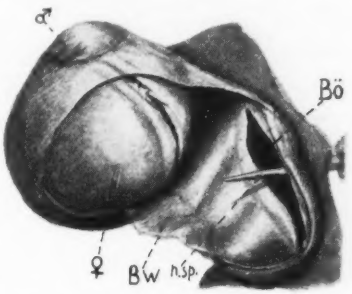



Fig. 26. Ascothorax—and below the distended wall of the bursa. The absence of any other envelopes is clearly visible. Likewise distinctly visible is the connection with the environing medium (a needle's end is introduced into the bursal aperture). Magnif. about 8 ×. *Bö*—bursal aperture; *Bw*—bursal wall; *n.sp.*—the point of the needle.

female in this position occurs presumably at the time when the animal is still of *small size* and has the ability of moving freely within the bursal cavity.

The parasite attaches itself to the wall in the following way: with the pointed end of the fifth antennular joint the female pierces the bursal wall in two places. Thereupon the hook like end of the fifth joint pushes into the bifurcation (the pleon of the fourth joint)—a fact I had occasion to observe on dissected infested ophiuroids and on sections (fig. 25 and fig. 2, plate II) Where the bursal wall has been pierced small swellings arise. The parasite is attached either by one or by both antennules.

c. *The males* have no constant position in relation to the female. They lie between the body of the female and the bursal wall. They may be found at any place. I sometimes saw males attached by an antennule to the bursal wall. The same has been noted in one case by DJAKONOV (1914, p. 163). It may be concluded from the variety in the orientation of the males which had come to our observation, that the males may move about; in this they are helped by the mantle valves, their mobile abdomen, and their strong antennulae which they can use for drawing their body up. The males likewise have a tendency of placing themselves close to the bursal aperture, where the animal finds the most favourable respiratory conditions.

d. *Special respiratory organs are absent.* In females the body surface together with the leaf like limbs—which by their movements produce a constant flow of water in the broad pouches—serves for respiration. It is to be presumed that respiration in males occurs in a similar way.

e. Ascothorax feeds on the damaged and desquamated cells of the bursal walls, and probably also on the coelomic liquid of the host. When the parasite takes in food the apical part of the oral pyramid is applied to the bursal wall, and the oral appendages penetrate into the tissues of the host. The maxillae damage with their pointed ends the epithelial wall of the bursa and the maxillulae, folded together so as to form a groove or small tube, penetrate into the wound thus produced. It is by way of the tubular maxillulae that the food is sucked in (fig. 3, plate II).

About the place where oral appendages penetrate into the tissues of the host a swelling arises, and damaged cells may be seen. We could trace the picture presented by the oral appendages during the process of sucking on serial sections of an infested Ophiuroid. The defecation takes place through the anal aperture. The fecal masses appear as small spherical clumps staining with borax carmine. In sections they may be found in the vicinity of the fifth abdominal segment.

f. The brood pouch of the female is left by the larva in its Ascothoracid stage. The larvae, on reaching the appropriate stage pass out by active movements out of the mantle cavity, thereupon they, depending on the orientation of the female, either move in the space between its body wall and the



VOL 27 194

bursal wall or leave the host passing directly from the mantle cavity out through the mantle slit. On an object appropriately fixed we saw the issuing larvae.

The Ophiuroid is infested by the larvae penetrating through the bursal slit. One brittle-star may evidently be repeatedly infested, as the Ascothorax found in the same specimen are not all of the same age. Presumably reinfestation of the host by larvae which have just passed out may take place.

g. *The presence* of Ascothorax ophioctenis causes castration of the host, and it was only as an exception that in infested Ophiuroids scarcely visible gonads could be discovered. The gonads contiguous to the infested bursa were always found to be castrated. The noninfested Ophiuroids secured together with the infested specimens always possessed well developed and functioning gonads. The very joung Ophiuroids alone had insufficiently developed gonads. Among the opened Ophiuroids (at the stations 63—19, IX, 1934) one hermaphroditic specimen was secured closely similar to the form depicted by THORSON (1934). The effect produced by Ascothorax on the host consists in abating the avtivity of its germinative glands. The castration being general and not partial it may be concluded that disappearance of the gonads is not due to the parasite, in other words that the parasite does not feed on them. The cause of castration must lie in the general exhaustion of the host as a consequence of the presence of the parasite. The influence of the parasite is so strong that the abortive development of the gonads in the Ophiuroids is produced by quite young Ascothorax specimens, such as have just penetrated into the host. Consequently it is to be concluded that this parasite feeds on the body juices of the host.

The other parasites occurring in Ehinodermata in respect of the character of their feeding and the effect produced by them in the host—may be classified in two groups: In 1) the *actively* castrating and 2) the *passively* castrating. The *first group* is represented by Protomyzostomum polynephris Fedotov which lives in the bursal cavities of the Ophiuroid Gorgonocephalus eucnemis. It feeds on the gonads of its host producing partial, or in cases of strong infestation—complete castration in the host (FEDOROV 1915). Among the Ascothoracida it is to the Dendrogasteridae that the gonads of the host serve as food. The larvae of Dendrogaster murmanensis Kluge penetrate into the host (Crossaster papposus) through the germinal opening and at first feed on the gonads producing partial castration (KLUGE, in litteris). Later on they migrate into the body cavity of the host and feed there on the coelomic liquid. The partial castration of Echinocardium cordatum Pennant seems to be produced in the same way by its parasite Ulophysema öresundense Brattström (1936). In other forms of Dendrogasteridae partial castration has been noticed by: FISCHER (1930), KORSCHELT 1933), JOSII (1931 a) and BRATTSTRÖM (1937).

Of the parasites which must be put into the *second category* (passive castra-

tion) the most striking instance is found in the Rhizocephala (Sacculina, Peltogaster and others).—These forms take up nourishment osmotically, feeding on the juices of the hosts body—the gonads are not directly attached by them. But their presence produces castration in the host by causing exhaustion of the host (SMITH and other more recent authors). The same effect on their respective hosts is produced by certain parasitating Mollusca, which do not attack directly the gonads of their host but cause their retarded development, or even produce complete castration. Entoconcha mirabilis MÜLLER (1852)—cited from SCHWANWITSCH 1917— castrates its host, the holothurian Synapta digitata. Entocolax ludwigi Voigt likewise does not feed on the gonads of Myriotrochus rinkii Stenstrup but brings about exhaustion of the body of its host, and subsequently castration involving in some instances all the germinal glands of the host (noted in 65 per cent of cases). When complete castration was observed the degree of infestation was always very high. In the cases when in the holothurians but one specimen of the parasite was contained the gonads had a more or less normal aspect. On the other hand, the noninfested Myriotrochus individuals always possessed quite normally developed gonads (SCHWANWITSCH 1917). Similarly the presence of the Mollusk Paedophoropus dicoelotius Iwanov parasitating in the respiratory trees and Poli's vesicles of the holothurian Eupirgus pacificus Östergren causes retardation of development in the gonads of the host although the parasite feeds solely on the cavital liquid (IWANOV, A. 1937).

This category of parasites includes also Ascothorax ophioctenis.

## V. COMPARATIVE SURVEY OF THE ASCOTHORACIDA.

The Ascothoracida group comprises nineteen species only and one of these is Ascothorax ophioctenis. The various Ascothoracida with different mode of life, have also different evolution and considerably varying structural characteristics. As compared with A. ophioctenis some of the forms are more strongly, whereas others are less conspicuously modified.

The two principal aims of this investigation are: 1) to establish the place belonging to A. ophioctenis in this group, and 2) to trace the way of evolution in the Ascothoracida. In view of this first will be given a comparative survey of the group and the end of the chapter will be dedicated to the conclusions which may be drawn therefrom.

### A. THE BODY FORM, SEGMENTATION AND APPENDAGES.

The shape of the body in various Ascothoracida varies in accordance with their mode of life. Their habitus is determined by the structure of the mantle

valves; the body proper of the animal is fixed by its dorsal side between the valves. The segmentation of the body in different forms presents various degrees of development and may even be fully absent. In accordance with the degree of mobility of the animal, and the degree of its parasitism the degree of rudimentation of the limbs varies.

### a. The body form and the mantle.

In the free living Synagoga mira Norman both body and mantle is bean-shaped; the mantle valves are flat and small and scarcely cover the body of the Crustacean: There is no sexual dimorphism—NORMAN (1912) indicates that it is very difficult to distinguish the females from the males by their form. The females has in its mantle a small depression serving for the rearing of the brood.

*Synagoga metacrinicola Okada*— the constant ectoparasite of Metacrinus rotundus Carpenter is about of the same shape as the form described above. Sexual dimorphism consists in that the males are smaller than the females and their valves are also smaller. In the females the valves cover the whole body and posteriorly in the dorsal portion of each valve—a depression—the brood pouch—is enclosed. As in S. mira branches of the gut diverticula and the gonads lie within the valves (OKADA 1926).

The above described Ascothorax ophioctenis has an exceedingly well expressed sexual dimorphism. The males are very small, their valves are fairly well developed, the body is bean shaped. The females are much larger, and their valves, extending laterally, present the aspect of two hemispheres. This extension of the valves is caused by the great increase in size of the brood pouches, this must be put in connection with the production of a more numerous brood—a circumstance due to the animal having grown endoparasitic. The massive portion of the valves are pushed forward and down.

Still more strongly modified are the *Dendrogasteridae* parasitating in the body cavity of starfishes. The difference in the habitus between female and male is more strongly accentuated. In the males the valves are still well developed, they coalesce only in their dorsal part where a short suture is present. Contrary to what is found in other forms the Dendrogasteridae males parasitate in the mantle cavity of the females. Their testes are exceedingly developed and fill out the posterior ends of the valves. These are extended and present the aspect of long sac-like prolongations. (KNIPOWITSCH 1892, LE ROI 1907 and my own—as yet unpublished— findings.) In conjunction with this circumstance the males have partially lost their mobility. In the *female* Dendrogasteridae the mantle is still more extended laterally than in the Ascothorax ophioctenis females. It appears either in the shape of a simple or double sac as in Ulophysema (BRATTSTRÖM 1936 and 1937) or consists of arboreous ramifica-

tions as in Dendrogaster and Myriocladus (KNIPOWITSCH 1890, JOSII 1931 a and other authors). Together with the branching of the mantle we find the branching of the gonads, the gut and the brood pouch; the brood pouch lies dorsal of the intestine and the gonads. The branching of the mantle in the Dendrogasteridae is presumably connected with the respiratory function: owing to the ramifications the surface in contact with the cavital liquid of the host is increased. The increase in size of the mantle is connected with the *increase in number of the embryos and the lengthening of the incubatory period.* The edges of the valves are coalesced nearly in their full extent; a small aperture alone remains through which the shears like claws of the antennules are periodically pushed forward, and out of which the apical end of the oral pyramid protrudes (OKADA 1925, JOSII 1931 a).

In the fam. Lauridae the mantle in the female individuals is extended dorsoventrally, and the animals presents the shape of a single (Laura) or a double (Baccalaureus) fairly thick plate. The edges of the mantle valves are all along fused together. A small aperture alone remains, it serves to connect the internal cavity with the surrounding medium. In the mantle a thick-walled massive portion, and a thin walled brood pouch are distinguishable. The walls are massive and in them regularly branching ovaries and intestinal branches are included. In the cavity between the valves the brood is incubated (LACAZE-DUTHIERS 1883, KNIPOWITSCH 1893, JOSII 1931 b, PYEFINCH 1934 and 1936). In the males of Baccalaureus (JOSII 1931 b and BRATTSTRÖM 1931 b) probably also in the males of Laura the mantle is bivalvate and has a short dorsal suture. Within the valves lie the gut diverticula and the testis. The males are very much smaller than the females, they live as ectoparasites and seem to have the ability of freely moving about. The immobile females live in corals below their sarcolemm.

It may be concluded from the above that the mantle of Ascothorax ophioctenis retains a fairly primitive structure; the mantle is distinctly bivalvate—a feature most clearly expressed in males. However in connection with the endoparasitic mode of life A. ophioctenis presents certain complications in its morphology—in females they are more strongly expressed than in males. These complications consist in that the valves are more massive which is due to the gonads being more strongly developed, also the brood pouches increase in size causing the mantle to spread in a postero-lateral direction. In the Dendrogasteridae the mantle is strongly extended laterally. Its bivalvate character stands out clearly in the mantle of the larvae of the ascothoracid stage, and the mantle of the males. In the males the bivalvate character of the mantle (though it is strongly extended laterally) is retained in full (KNIPOWITSCH 1892, LE ROI 1907, JOSII 1931 a).

In Petrarca the mantle is distinctly bivalvate (FOWLER 1890).

In the fam. Lauridae the mantle extends in the dorsoventral direction. In



VOL.
27
1946

the Lauridae as in the above discussed forms the original type is represented by a bivalvate mantle as found in the males of Baccalaureus (Josii 1931 b) and of Laura (Lacaze-Duthiers 1883).

The mantle in various forms presenting no uniformity in the course of its evolution the inference is that the evolution occurred in two different directions: 1) a lateral extension as in the Synagogidae and Dendrogasteridae —in this series A. ophioctenis must be put between the genera Synagoga and Ulophysema and 2) a dorso-ventral ramification such as is found in the fam. Lauridae. In both cases the original form is represented by a bivalvate mantle with relatively small valves, joined together by a short dorsal suture. In both these series the primitive structure of this organ is retained longer in the males.

### b. The segmented body.

The segmented body lies enclosed between the valves. It fuses with the valves dorsally and laterally in its cephalic portion. The characteristic repartition of the body in distinct portions may be noted in all Ascothoracida. The variations in the number of body segments are relatively small. The Synagogidae and Dendrogasteridae possess 16 segments, the Lauridae 15.

The cephalic portion is always constituted of five[1] segments which are fused together and bear four pairs of appendages: antennules, mandibles, maxillulae and maxillae. The last three form part of the oral pyramid.

The thoracic portion includes six segments; as a rule its segmentation is distinctly visible. In Baccalaureus the first two thoracic segments are fused with the cephalic portion and have lost their appendages. Four segments only remain free (Josii 1931 b, Pyefinch 1936). In the genus Myriocladus segmentation has entirely disappeared (Okada 1925) while in Dendrogaster astericola the segments are retained in a rudimentary form as represented by 10 distinct tubercles. In Ulophysema öresundense and U. purtalesiae the body is feebly segmented (Brattström 1936 and 1937).

The *abdominal portion* in the Synagogidae includes five segments and bears a furca. The Lauridae have four segments besides the furca. In the Dendrogasteridae it is likewise composed of five segments—one may judge of it by the larvae of Myriocladus (according to my findings), and those of Dendrogaster and Ulophysema (Knipowitsch 1892, Brattström 1936)—when they are in their as—cothoracid stage. In the reproductions of Ulophyseme (given in Brattström's paper) and of Dendrogaster (Knipowitsch's work) 5

[1] The question of the number of cephalic segments in the Crustaceans is not quite clear. Some authors ascribe 6 segments to it, others 5. It is the latter number that seems to me the correct one, as in the symposia on Copepoda and Cirripedia 5 cephalic segments are mentioned. (Presumably always the acron—the preantennular segment—is not taken in consideration). Paired eyes in all three suborders being absent it may be concluded that the point of view here given is permissible.

abdominal segments may be counted, although the authors named consider them to be in the number of four.

The tubercles that KNIPOWITSCH found on the ventral side of the body in Dendrogaster likewise serve to corroborate our point of view that the body of the Dendrogasteridae is composed of 16 segments.

According to the character of its segmentation Ascothorax ophioctenis is a typical member of the family Synagogidae. Its body is composed of 16 well developed segments.

## B. THE APPENDAGES.

### a. The antennules. Their structure.

A full description of the antennules exists only for Synagoga mira—NORMAN (1912). According to OKADA (1926) it may be inferred that in S. mira and S. metacrinicola the antennules are very like in their structure. NORMAN indicates that the antennules have six segments they are of the nature of grasping appendages and their musculature is exceedingly abundant.

The *first* joint is long and smooth. The *second* is jointed onto the first, forming an angle with it and bears a patch of setae on its ventral side. The dorsal side is smooth. The *third* joint is triangular; the proximal portion of its dorsal surface is setose. The fourth joint is short and triangular, it has a long ventral and a short dorsal margin. In the anterior portion of the dorsal edge lie two dents, and in the proximal portion—two spines, thick and jointed. Onto these dents and bristles the anterior end of the sixth joint is reflected. The *fifth* joint has a greater length than the dorsal edges of the two last described joints taken together. It is covered along its upper margin with long plumular bristles. The *sixth* is of the same length as the fifth; its dorsal edge bears neither setae nor bristles. The ventral side possesses additional structures. It possesses midway an articulated bristle and a lobular appendage (fig. 27, *1*, *2*) articulated onto a common base. The lobe bears 3 spines at its ends. In the anterior portion of the joint lies a lobule articulated with the joint (fig. 27, *3*), it has 3 terminal bristles. The sixth joint is terminated by a simple claw which is setose on its inner surface and possesses one small bristle; the end of the claw curves upward (fig. 27, *4*).

In Synagoga mira and in A. ophioctenis the antennules present a great similarity in the distribution of their muscles; this is especially the case in the III—VI joints; onto the movable claw, at the end of the VI joint a fairly strong muscular strand is attached—it is more mighty than that of A. ophioctenis. The same may be said of the other muscular strand attached to the articulated seta (*1*). The flexor muscle of the VI joint is very strongly developed. It attaches to the ventral margin of the V joint. The extensor muscle is composed, as in A. ophioctenis, of three strands; they run along the



VOL
27
194

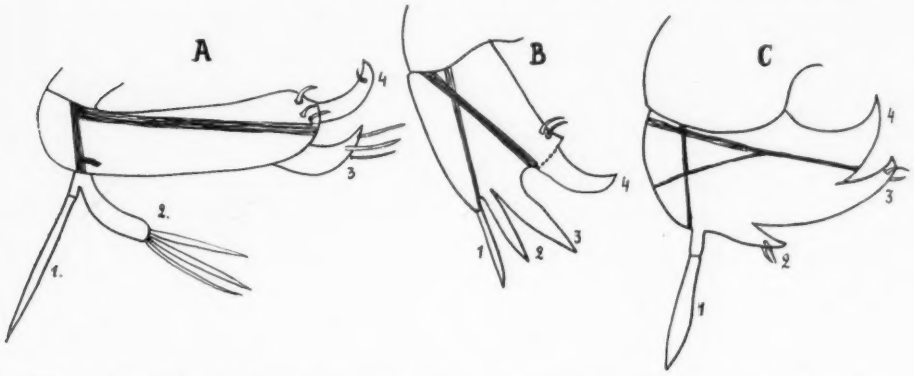



Fig. 27. Terminal joints of. *A*—Synagoga; *B*—ascothoracid larva of Ascothorax; *C*—adult Ascothorax; *1—4*—the appendages in the order of their sequence.

V and IV joint and attach in the third joint. In the fourth joint (according to the drawing) no insertion of muscles takes place; all the muscle strands simply pass through the segments. In the Dendrogasteridae the antennules have four joints and are of the grasping type. The disposition of the musculature indicates that here considerable translocations and fusion of the joints have taken place (Josii 1931 a).

The first two joints are very broad and possess strong muscles which set in motion the terminal portion of the antennule; this portion consists of two joints—the third and the fourth; the fourth joint is much narrower than the third, very mobile and may be reflected onto the third. It bears very numerous additional structures—their character and distribution proves that the IV joint in Myriocladus is homologous with the VI joint of Synagoga, while the hook in the antero-dorsal angle of the IV joint in Myriocladus is homologous with the movable claw in Synagoga. This is the more probable as a muscle is attached to the base of the claw (fig. 27). The fourth joint possesses a strong double adductor muscle and a less considerable simple abductor. The muscles are attached partly to the posterior margin of the third joint and partly to its ventral margin (fig. 28).

The antennules composed of five joints in Ascothorax ophioctenis (see chapt. IV) take up an intermediate position between the antennules of Synagoga and those of Dendrogasteridae. This may be proved by a comparison of the homologous parts.

The apical joints in the antennules in Synagoga and Ascothorax possess the same number of additional structures and a coincidence in the distribution of their musculature may be noted. This stands out most clearly if developmental data are taken into consideration. In the course of their development the antennules of Ascothorax pass through two stages: 1) The larval stage (ascothoracid larva) when the antennules are very like these of Synagoga. The apical

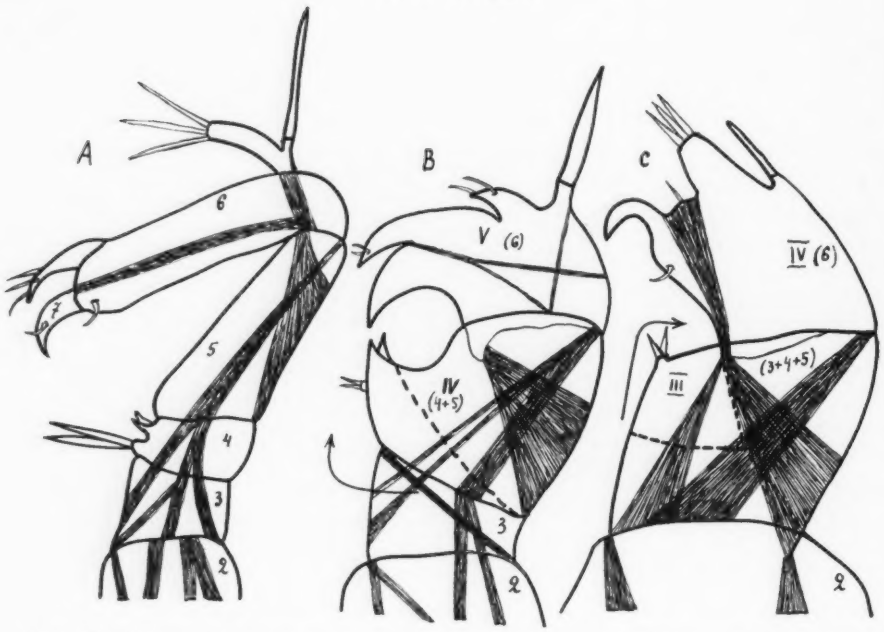



Fig. 28. Diagram of antennules of: *A*—Synagoga; *B*—Ascothorax; *C*—Myriocladus. A. 2—7—of the joints in the order of their segment. B. 2—6—joints homologous with those in Synagoga in the order of their sequence. Dotted line—place of the supposed fusion; arrow—direction in which tapering took place; roman numbers—the joints in the antennules of Ascothorax in the order of their sequence. C. Lettering as in B.

joint is quadrangular. At its anterior end lies an articulated claw, to the base of which, as in Synagoga a muscular bundle is attached. There is the same analogy in the distribution of the other additional structures. In both instances a muscular bundle very similar in its aspect is attached to the articulated bristle. 2) After metamorphosis the structure of this joint is modified—it loses its quadrangular shape and becomes triangular; its end curves upward. The terminal claw (fig. 28, *4*) coalesces without producing a suture with the body of the joint. The common basis proper to the articulated bristle and the posterior lobule fuses with the body of the joint and they become distinct. The musculature retains its typical distribution as found in the larvae of the ascothoracid stage and in Synagoga. In view of the complete coincidence here indicated there can be no doubt that a homology exists between the apical joints of Synagoga, Ascothorax and Dendrogaster. As a most convincing proof of this circumstance may be considered the recapitulation of the structure of the joint in the larvae of Ascothorax, as well as the fact that in the adult the distribution of the muscles in their apical joint is retained. The disposition of the adductor and abductor muscles in the segment in Ascothorax indicates that here the joints are fused together and, owing to it, the number of the segments has come to be reduced from 6 to 5. The extensor muscles of the VI joint in

Synagoga are attached to the dorsal margin of the VI joint. In the IV joint there is no insertion of musculature—the muscles just traverse it (fig. 27). In Ascothorax the extensor muscles of the V joint (homologous with the VI Synagoga joint) is also attached to the III joint (fig. 28). The flexor muscle of the VI joint in Synagoga is attached to the ventral margin of the IV joint and reaches up to where it is articulated with the IV joint. In Ascothorax the flexor of the terminal V joint is attached to the ventral edge of the IV joint and reaches up to its articulation with the III joint. As the IV joint in Synagoga possesses no insertion of muscles, and as the joint has no musculature of its own it may be said that this joint is on its way to coalesce with the V joint. This is what must have occurred in the Synagoga-like ancestor of Ascothorax. The IV joint in Ascothorax is homologous with the IV + V Synagoga joint. The fusion must have occurred in the following way. The ventral edge of the IV joint suffered partial reduction, it came to be somewhat shifted and became part of its posterior edge, contiguous with the III joint. At the same time the posterior lower corner of the V joint came into contact with the anterior lower corner of the III joint. The body of the V joint grew shorter and considerably broader. The dorsal edge of the IV joint having prolonged itself wedgewise the joint has increased in length and its additional structure shifted to its anterior end (fig. 27). The double dentiform process has come to lie in the anterior angle and the two articulated bristles which primarily belonged in the hind angle of the segment were equally shifted forward and have come to lie in the anterior angle of the joint, immediately behind the double dentiform process. The dorsal margin of the fifth joint fused with the fourth changed into a platform lying between the dorsal angle and the articulation joint formed with the apical joint. Consequently, by dint of comparison, we learn to recognise that in Ascothorax the incurved portion of the anterior edge of the IV joint has its origin in the very much shortened dorsal edge of the V joint of the Synagoga-like ancestor. The fusion of the joints may be proved only by comparison of the homologous parts, as a border line between the fused segments does not make its appearance even in larvae of the ascothoracid stage. The morphological modification of the Ascothorax antennules is the result of these complicated shiftings. It changed from the primitive shears like claw—the Subchela in Synagoga—into the *Chela* proper to Ascothorax. This was due to the downward shifting of the articulation formed with the apical joint. The dorsal angle of the IV joint in Ascothorax bearing the double dent became a p l e o n, the apical segment a d a c t i l u s. At the same time the grasping organ has grown stronger, while the lever in the apical (V) and the IV joint grew shorter. The musculature retained the degree of development found in Synagoga.

The origination of a four jointed antennule in the Dendrogasteridae (Myriocladus) is a continuation of the process found in Ascothorax. Here also we

have fusion of the joints and they are stretched in the form of a wedge. In Myriocladus the complex III joint is the result of fusion of the III, IV and V joints of the Synagoga-like ancestor. This is to be concluded from the fact that the muscles governing the movements of the terminal (IV) joint in Myriocladus is attached in the penultimate (III) joint. That such a process may take place may be inferred, as in Ascothorax the articulation between the III and IV joint is unmovable, while the muscles which have the governing of the IV joint are rudimentary. All this speaks in favour of the point of view that in Ascothorax the articulation between the III and IV joints is on the point to disappear (see chapt. IV). In the Dendrogasteridae the III and IV joints of the Synagoga like ancestor coalesce, and their common ventral end has grown shorter.

Together with these alterations—changes in the dorsal edge also occur. The dorsal edge pushes further forward and the place of the double dentiform process is taken up by the bristles articulated at their base. The dentiform process is reduced and forms part of the anterior edge of the joint (fig. 27 c).

It may be concluded from the above that in the series of the modifications just discussed Ascothorax must be given a place midways between Synagoga and the Dendrogasteridae. An analysis of the apical joint of the Synagoga antennules indicates that in the ancestor of this form the joints were not less than seven in number, it being impossible to consider the movable simple claw otherwise than a vestige of a VII joint.

On studying the structure of the antennules in the males of Baccalaureus japonicus we arrived at the same conclusion. The drawing and description given in Josii's paper (1931 b) show that in the Baccalaureus japonicus males the antennules have six joints disposed in a row, the apical joint bearing a simple claw. This claw must be considered as a rudiment of a seventh joint. The structure of this type of antennules indicates that three joints—and not two as in Synagoga and Ascothorax—participate in the grasping function. This type of structure is proper to the most primitive form of claws—the *prochela*. Unfortunately Josii's paper here cited contains no descriptions either of the musculature or of the function of the antennules in the males of Baccalaureus japonicus.

The female Lauridae possess rudimentary antennules composed of three joints (Lacaze-Duthiers 1883, Knipowitsch 1892, Josii 1931 b). Their first two joints are simple, the apical (III) bears a claw and an articulated spine. It is probably homologous with the apical segment of the males of this family and other forms belonging to the Ascothoracida, but a definitive answer to this question cannot be obtained as it is also impossible to decide in what way the fusion of the joints takes place.

The description given of the three jointed antennules of Petrarca bathyactidis



VOL.
27
194

is not detailed enough, and this renders difficult their comparison with the antennules of other Ascothoracida.

It follows from our survey that in the group under discussion the evolution occurred in two different ways which fully coincide with the ways in which the mantle developed. The one was represented by the development of such forms in which the antennules in both sexes present the same structure, while the oligomerisation is connected with an intensification of the function of the antennules and a progressive development of this organ (the Synagogidae and Dendrogasteridae). The other direction is characterised by the development of the antennules in the Lauridae. It must be noted in the first place that in females and in males the organ is differently developed. The males possess well developed antennules of the Prochela type, while in the females they are distinctly rudimentary. The fact that these two branches developed independently of each other is corroborated by the structure of the antennules in the males of Baccalaureus, whose antennules are more primitive than those of Synagoga. Consequently it may be considered that the Lauridae are more closely connected with the original form—in which the antennular joints had a linear disposition—than the Synagogidae or the Dendrogasteridae.

The organs described by PYEFINCH (1934 and 1936) in Baccalaureus maldivensis and B. hexapus, as antennules, and designated by BROCH (1929) in B. japonicus as horn-like processes are either a modified first pair of thoracic limbs (JOSII 1931 b) or, I should say, more exactly—dorsal protrusions of the thorax serving as support to the mantle valves. This question requires to be reinvestigated and must be verified in all its details. But already at the present moment it is certain that these formations are not antennules. The more so as JOSII has described true antennae in Baccaluareus japonicus. BRATTSTRÖM (1936 b) likewise considers the horny processes in Baccalaureus as homologous with the dorsal excrescences of Ulophysema, and consequently also of Ascothorax.

### b. The antennae.

The Ascothoracida—not the adult forms alone but the larvae also—possess no antennae. The only instance I know of antennae having been described is indicated by PYEFINCH (1936) for Baccalaureus hexapus. The description of this phylogenetically so very important organ, given by this author, is based on reconstructions. As the organs under discussion are disposed close to the oral pyramid Pyefinch infers that they are true antennae and not antennules. The characteristic given of this organ is due to the circumstance that the author cited considered the horn-like processes to be the antennules. We find however positive proof of the erroneousnes of this point of view in the investigation of JOSII (1931 b), who in females of Baccalaureus japonicus Broch saw,—together with the horn-like processes—rudimentary antennules lying on both

sides of the oral pyramid; they consist of three joints and ar similar to those which occur in the Laura gerardiae females. Now, if we accept PYEFINCH'S (1936) point of view, it would mean that the genus Baccalaureus, and with it all Ascothoracida possess antennae. However in spite of his statement concerning the antennae this author does not hesitate to consider B. hexapus as belonging to the Cirripedia Ascothoracica.

### c. The oral apparatus.

In all Ascothoracidae the oral pyramid is more or less similar in structure. The labrum in both Synagoga species has the same aspect as that of Ascothorax, with that difference that it does not envelope the oral appendages or with its hind edges and that it bears a patch of fine setae on the outer surface of its anterior end (NORMAN 1912).

In the other forms, including Ascothorax, the oral pyramid is entirely bereft of either setae or spines. In all—Ascothorax and Synagoga excepted—the hind edges of the labrum fuse together forming a tubular sheath about the oral appendages (KNIPOWITSCH 1892, LE ROI 1907, OKADA 1925, JOSHI 1931 b).

The *mandibles* in Synagoga are well developed and their outward margin is covered with setae. Their terminal portions are broadened, they are of triangular shape and bear stout spines on their inner margin. In Ascothorax the mandibles are still large but present already traces of rudimentation and do not protrude out of the sheath.

In the Lauridae the mandibles are represented by a pair of vestigial chitinous dents (KNIPOWITSCH 1892, PYEFINCH 1934 and 1936, JOSHI 1931 b).

According to the description of various authors the mandibles in the Dendrogasteridae may be present or absent. Distinct evidence of their absence has been obtained only for Dendrogaster astericola (KNIPOWITSCH 1892). In regard of the genus Myriocladus the data are contradictory. In Myriocladus (see Dendrogaster arborescens Le Roi) no mandibles were found by the author who has described this form. (LE ROI 1907.)

On the other hand, in OKADA'S work (1925) treating of another species belonging to this genus, mention is made of the existence of feebly developed maxillae and JOSHI (1931 a) has definitely established the presence of mandibles in many forms of this genus.

The *maxillulae*. The structure of this organ in Synagoga mira is most complicated. They possess simply pointed ends. Along their anterior edge the maxillulae in the females are covered with hairs which at the base of the maxillulae change into spines joined together by a chitinous membrane (1912). In Ascothorax the maxillulae present a somewhat different aspect—they are composed of a completely smooth body and groove like ends elongated into a long proboscis. Within the Lauridae a morphological series may be set up

beginning with the well developed maxillulae of Laura gerardiae and ending with their complete reduction in Baccalaureus hexapus, while Baccalaureus japonicus and B. maldivensis belonging in this series take up an intermediate position. (PYEFINCH 1936.)

The *maxillae* are paired in Synagoga; they are not fused together (NORMAN 1912, OKADA 1925). They bear spines along their posterior margin and a double point at their anterior end. In Ascothorax the maxillae are paired and fused together; in adults they are simply pointed and in the larvae of the ascothoracid stage they are coalesced only at their base while their ends possess a double point which after metamorphosis changes into a single one.

We have here a case of recapitulation of ancestral characters by the Ascothorax larva. The Lauridae have all well developed maxillae, which coalesce along their inner margin the apical portions alone remaining free. In Dendrogaster astericola they are fused in their length, their ends alone remain free (KNIPOWITSCH 1892). In Myriocladus, according to LE ROI (1907) the maxillae are well developed, while the maxillulae are rudimentary. OKADA (1925) is of opinion that the maxillae are nearly quite atrophied and lie at the base of the maxillulae; such is also JOSHI's (1931 a) point of view. Which of these two opinions is the right one must be proved by further investigations. It is impossible to indicate the topography and to establish the exact number of appendages in Petrarca bathyactidis. The mandibles mentioned by FOWLER (1890) correspond probably to the maxillulae or the maxillae. On the animal adopting the parasitic mode of life the oral apparatus undergoes certain changes. The posterior edges of the bilobed labrum fuse together forming a tubular sheath for the oral appendages. The maxillae which in Synagoga are free—here are coalesced; the mandibles and maxillulae undergo gradual reduction. The primarily piercing oral apparatus (Synagoga, Ascothorax) changes into an apparatus of the sucking type—in the Dendrogastridae and certain Lauridae. The initial stages of these modifications occur in Ascothorax in which the mandibles do not protrude any more beyond the edges of the sheath and the maxillae fuse together. The highest degree of modification is proper to the Dendrogasteridae and Lauridae.

In Synagoga metacrinicola a small prolongation covered with spines which lay anteriorly to the first pair of thoracopodia was described by OKADA (1926). NORMAN (1912) described in Synagoga mira special additional structures localised to the fore of the first pair of thoracopodia. According to this author they serve to conduct the eggs into the brood pouch. In Ascothorax similar formations could not be found but I found a pointed patch of spines lying anteriorly to the first pair of thoracopodia (fig. 14). In the absence of comparative data it is difficult to decide on the character of these spines and whether in the patch mentioned they are homologous with the processes existing in S. metacrinicola.

### d. The appendages of the thoracic portion.

*The limbs belonging to the thoracic portion* are in the genus Synagoga alone quite typical natatory biramous appendages. Each of the six pairs possess a jointed ecto- and endopodite, both rami bearing long natatory spines (NORMAN 1912, OKADA 1926).

In Ascothora the limbs are distinctly rudimentary although they frequently remain biramous. In the females they are leaf shaped and—the first pair excepted—biramous. In the sixth pair it is the exopodite only that is articulated while the endopodite is fixed on the protopodite. In the second and the fifth pair the exopodites are composed of two joints; the endopodites, though mobile, are constituted of one joint. In the second and the fourth pairs both branches contain two joints. In the males the appendages, though still retaining their natatory character, are more considerably reduced. The III and IV pairs alone are biramous, in the II and V pairs the endopodite is to a great extent reduced and coalesces with the basipodite, the exopodite is jointed and mobile. In the VI pair an exopodite alone is present. The I pair has no branches at all and is represented only by a protopodite composed of two joints. In larvae of the ascothoracid stage all limbs are biramous and belong to the type of natatory limbs. The first pair is rudimentary. Their branches, constituted of but one joint are very small in size—especially the non articulated endopodite. In the other limbs both branches are jointed and bear long natatory spines. The females of Ulophysema possess but 4 pairs of limbs. These are considerably reduced and present the aspect of tubercles (the males are so far unknown). The larvae in the ascothoracid stage like all larvae of the Dendrogesteridae, have five pairs of biramous natatory limbs. The females of Dendrogaster have no limbs whereas the larvae possess five pairs of biramous limbs. Nothing is known of the limbs of the males (KNIPOWITSCH 1892). In Myriocladus (OKADA 1925, JOSHI 1931 a) the female has no limbs. The males possess five pairs of limbs similar to those of the larvae in the ascothoracid stage. In both cases the appendages are biramous a fact I have frequently had occasion to note on my mounts. In Baccalaureus japonicus the males have six pairs of natatory well developed appendages. The second, third and fourth pairs are biramous, the others are uniramous and in each limb the protopodite is composed of three joints (?) (JOSHI 1931 b). The Baccalaureus japonicus females have four pairs of leaf shaped limbs composed of one joint and are more or less equally developed. In other forms belonging to the same genus the last pair is either rudimentary (B. maldivensis) or has completely disappeared (B. hexapus), so that only three pairs of thoracic limbs are present (PYEFINCH 1936).

JOSHI (1931 b) is of opinion that the horn-like processes and the pterygoid prolongations behind them, found in Baccalaureus japonicus, are modified



VOL
27
194

thoracopodia, and consequently speaks of the Baccalaureus japonicus females as possessing six pairs of thoracic limbs. In the Lauridae family six authentic pairs of thoracopodia exist only in the females and males of Laura gerardiae (LACAZE-DUTHIERS 1883 and KNIPOWITSCH 1892) and in the males of Baccalaureus. It is as yet difficult to decide what the horn-like processes represent, but they are quite certainly not antennules as PYEFINCH (1934, 1936) considers them to be. Whether they are thoracopodia or dorsal processes of the thorax—such as were described in Ulophysema (BRATTSTRÖM 1936) and in Ascothorax (STEPHENSEN 1931 see also chapter IV of the present paper)—this question may be solved only by detailed verification. Both points of views are quite plausible. Petrarca bathyactidis has six pairs of uniramous nonarticulated thoracopodia (FOWLER 1890).

VOL. 27 1946

In all the Ascothoracida which have grown endoparasitic a reduction of the thoracopodia takes place and they may even fully disappear (the females of Dendrogaster and of Myriodacladus).

In the males reduction also occurs; however, it is but partial and as a rule it consists in that some of the limbs lose their biramous character (Ascothorax). A full disappearance of one pair of limbs is observed only in the Dendrogasteridae males. This family is generally characterised by its possessing even in the ascothoracid stage—5 pairs of thoracic limbs (KNIPOWITSCH 1892, BRATTSTRÖM 1936 and my own findings). In this instance reduction of the first pair—and not of the last pair as BRATTSTRÖM (1936) supposed must probably have occurred. I judge by the fact that in the larva—at the ascothoracid stage—of Ascothorax ophioctenis it is the 1 pair that is most strongly reduced.

The process of rudimentation and atrophy of the limbs in the Lauridae seems to take a somewhat different course. It is not the first but the sixth pair of limbs that disappears. This is especially clearly visible in the genus Baccalaureus in which all graduations from a well developed sixth pair of limbs (Baccalaureus japonicus) to its complete disappearance (B. hexapus) may be found. On the other hand, if JOSHI's (1931 b) point of view proves to be erroneous and the horn-like and pterygoid processes will be found not to represent modified thoracopodia but to be something else, in that case the reduction of the limbs in the hind end will have to be considered as a continuation of the process of limb reduction begun and already terminated at the anterior end, as the first two pairs of thoracic limbs in Baccalaureus are as a matter of fact absent.

We may find a corroboration of the latter hypothesis in the manner in which —in the limbs—the biramous character disappears; this process consists in that in the first and last pairs the endopodites disappear. The degree of development of the endopodites increases towards the middle limbs—this may be observed f.i. in the males of Baccalaureus japonicus, JOSHI (1931 b), and in Ascothorax ophioctenis (see chapter IV of the present paper).

All the larvae known to us possess in their ascothoracid stage typical natatory biramous limbs and their protopodite is composed of two joints. In respect of this character, as in several others, they recapitulate the characteristics proper to their ancestors. Concequently it may be inferred that the Ascothoracida ancestors had biramous natatory limbs and that their protopodite was composed of two joints. The origin of the protopodite in the limbs of Baccalaureus japonicus which is composed of three joints is to me not clear. This might be a secondary phenomenon (?).

In respect of the structure and the number of their thoracic limbs Ascothorax is a form most closely related to Synagoga. Owing to the endoparasitic mode of life of the animal the limbs in Ascothorax came to be somewhat reduced though retaining on the whole their biramous character.

## C. ANATOMY.

### a. The integuments.

Both the body, and the mantle valves are covered with a chitinous layer of various thickness. The limbs, especially in the antennules, the furca and the outer surface of the mantle possess a thicker chitin than the body proper, and the inner face of the mantle. PYEFINCH (1936), in his description of Baccalaureus hexapus, mentions this fact and the same has been noted by me for Ascothorax ophioctenis (see chapter IV of the present paper). Further the chitin is thicker in the places of attachment of the muscles and at the pointed ends of the oral pieces and the antennules. This is represented in the figures given by JOSHI (1936 a) and is indicated also by me (see chapter IV of the present paper).

The chitin has the complicated structure proper to that of all Crustaceans. In Baccalaureus hexapus it is composed of two layers. When the Mallory stain is used they are found to be coloured differentially: the colour of the outer—cuticular—layer is red or orange, that of the chitinous layer is dark blue. The chitinous covering in A. ophioctenis is likewise composed of two layers, but the layer which takes on the red colour has come to my view in the antennules only, and nowhere else. In all other places I saw only the layer which stains dark blue—but this layer was found likewise to be of a complex structure—a fact not mentioned by PYEFINCH (1936). The outer chitinous layer takes on an intense light blue colour whereas the inner layer stains more feebly. The chitinous layer reposes, on the hypoderm represented by an even layer of cuboidal cells.

b. The nervous system and the organs of sense.

It has so far been impossible to establish the exact number of the ganglia of wich the abdominal mass in composed. For this reason and also in view of the similar structure of the nervous system in all the forms so far known of the Ascothoracida it is difficult to make a comparative analysis of the system. For this reason we shall give here only a general survey of all existing data regarding the morphology of the nervous system in various forms of this group.

In Synagoga metacrinicola Okada (the only form in this genus for which a description of its anatomical structure has been given) the nervous system is composed of a supraoesophageal ganglion connected by circumoesophageal commissures with the suboesophageal mass. From this mass arises a long nerve extending backwards (Okada 1926). Laura gerardiae has a supraoesophageal ganglion from which arise two circumoesophageal commissures connecting it with the suboesophageal ganglion. A narrow stricture separates the suboesophageal ganglion from the rest of the abdominal mass. The stricture lies immediately below the adductor muscle of the valves. In the region of this muscle the abdominal mass sends out two mantle nerves (Knipowitsch 1892). In Baccalaureus japonicus the nervous system has about the same structure. Josii found no mantle nerves. In Baccalaureus hexapus Pyefinch (1936) described—in addition to the usually occuring and already mentioned in other Lauridae (parts of the nervous system and the stricture below the adductor muscle of the valves) three lateral swellings which do not coincide with the inner metamery. The abdominal mass sends out a pair of nerves. These the author designated as the adductor muscle nerves. Judging by their location these nerves correspond to the mantle nerves in Laura gerardiae. In Petrarca bathyactidis the nervous system is composed of a small supraoesophageal mass, of circumoesophageal commissures containing nervous cells, and of an abdominal nerve cord, abounding in nervous cells but presenting no differentiation in ganglia. From this nerve cord numerous nerves running in the dorsal direction arise (Fowler 1890). More precise designations of these nerves are not given by the author. In Dendrogaster astericola the nervous system has a structure similar to that of the forms mentioned above. One pair of lateral trunks runs towards the mantle valves. Below the adductor muscle the nervous system forms a stricture (Knipowitsch 1892). The genus Myriocladus Okada alone presents certain variations. These are: absence of a stricture in the considerably shortened suboesophageal mass. A pair of nerves arises from the back part of this mass. The absence of a stricture stands in connection with the absence of an adductor muscle of the valves (Le Roi 1907). The nervous system in Ascothorax ophioctenis is on the whole similar to that of Synagoga and the Lauridae. In addition to the central nervous system our species posses-

ses 3 pairs of lateral nerves: the antennular, buccal and mantle nerves (see chapt. IV).

No organs of sense are present. The adult Ascothoracida have no eyes and static organs are likewise absent. The only tactile organs are the various hairs and spines on the antennules and the furca.

### c. The alimentary system.

In all Ascothoracida the alimentary system is composed of two parts: the gut which ends blindly or possesses an anal opening, and the gut diverticula which branch within the mantle and may be strongly developed.

In Synagoga metacrinicola the gut, according to OKADA, is composed of three distinct portions. The ectodermal oesophagus begins in the oral pyramid. It opens into the mid-gut protruding into its lumen in the form of a rounded "caput". The mid gut runs all along the thoracic region, a stricture delimits it from the hind-gut. The hind-gut opens outwards, the anus lies between the furcal branches.

The anterior portion of the mid-gut (the stomach) presents a swelling delimited by a broad stricture from the rest of the mid-gut. The gut diverticula arise from the stomach, extend towards the mantle valves, and branch within the mantle. OKADA (1935) gives no detailed account of these ramifications. However, judging by the figure this author gives of them, the main ramifications give off anterior and posterior branches of second order.

In Ascothorax ophioctenis, as in Synagoga, the gut is composed of three parts and opens outwards likewise between the furcal branches. The mid-gut alone has a somewhat different structure as it presents no gastric swelling.

The gut diverticula arise from the anterior portion of the mid-gut. In their number and topography the sexual dimorphism of the species finds itself reflected (see chapt. IV). The males have two pairs of branches—a short frontal and a long lateral branch. This last pair divides within the mantle in a fore and hind branch of second order from which blind diverticula—branches of the third order arise. The females have three pairs: a frontal, a lateral and a dorsal pair—the latter is not present in the males. These diverticula ramify more strongly than in the males and from the branches of the third order blind branches are frequently found to arise. The gut diverticula lie otherwise than in the male, as, owing to the strong development of the blood pouches, the massive portions of the valves are shifted forwards and downwards. In Petrarca bathyactidis the gut ends blindly. It is composed of an oesophagus and a mid-gut. The hind-gut is reduced. The gut diverticula are of two types—paired lateral diverticula which branch within the mantle valves and unpaired—a frontal and a dorsal—diverticula. The frontal branch runs forward of the gut along the medial line, the dorsal keeping close to the medial



VOL.
27
194

line takes an upward and backward direction—it arises from the dorsal wall of the mid-gut behind the region where the oesophagus opens into the mid-gut (FOWLER 1890).

Laura gerardiae has a gut opening outward and composed, according to type, of three portions—the fore, mid- and hind-gut; the anus lies between the furcal branches. The anterior portion of the mid-gut is somewhat widened; from it arise two large lateral gut diverticula; each of these divide within the mantle into two—a fore and a hind—branches of second order; these in their turn send off blindly ending ramifications towards the margin of the fused valves (LACAZE-DUTHIERS 1883, KNIPOWITSCH 1892). This is the original type of ramification for all the Lauridae. We meet with it in Baccalaureus japonicus in which the gut opens outwards—its gut diverticula are similar to those in Laura gerardiae (JOSHI 1931 b). In B. maldivensis and B. hexapus the gut and the gut diverticula have a somewhat different structure. The anal opening has disappeared and the ramification of the gut diverticula is quite peculiar. One of the branches of second order—presumably the anterior branch—has become quite reduced, while the other (the posterior branch) has attained a considerable development and penetrates, strongly ramifying on its way, into the spiral coils of the mantle valves (PYEFINCH 1936).

In Dendrogaster astericola likewise the gut ends blindly and is composed of an oesophagus and a mid-gut. The oesophagus has a chitin lining. The mid-gut is not lined with chitin; it has a characteristic histological structure very similar to that found in Ascothorax ophioctenis (see chapt. IV). From the anterior part of the mid-gut arise two gut diverticula; they separate each into a fore and a hind branch which send off blind diverticula into the corresponding mantle "arms" (branches)—KNIPOWITSCH (1892).

In Myriocladus, as compared with Dendrogaster, the ramification of the gut diverticula is more intricate. The fore and hind branches produce branches of the third order which either end blindly or give off still finer diverticula. The topography of the branching of the arms and the gut has been analyzed in detail by JOSHI (1931 a). Histologically the alimentary system of Myriocladus is closely similar to that of Dendrogaster.

In summing up the data regarding the morphology of the alimentary system of the Ascothoracida the following may be noted. 1) The original and most primitive mode of ramification consists in the formation of lateral gut diverticula which separate within the valves into fore and hind branches of the second order. 2) This type of branching is retained in full by the females of Baccalaureus japonicus and Laura gerardiae. In the males of Ascothorax ophioctenis the branching is already more complicated as frontal diverticula make their appearance; still more complicated are the ramifications in the females of this species through the appearance of dorsal diverticula, and by reason of the massive portion of the mantle being shifted forward and causing

in consequence considerable modifications in their topography (see chapter IV). In Petrarca bathyactidis we also meet with secondary structural complications represented by unpaired diverticula. In the Dendrogasteridae the gut has nearly in full retained the primitive type of branching, as it has no others, but only lateral, branches. These branches attain in their development the highest degree of complication and are a typical progressive organ. 3) The modifications in their topography and the appearance of secondary gut diverticula such as the paired and unpaired frontal and dorsal diverticula stand in direct relation to the structure and form of the mantle valves. When the animals change to a parasitic mode of life, especially when they become parasites of the body cavity (Dendrogasteridae) and the tissues in corals (Lauridae) the gut closes and the hind gut is reduced while the mid-gut becomes sac-like. 5) In the Ascothoracida ancestors the gut did not end blindly. The gut diverticula were represented by one pair of lateral diverticula, which separated into a fore and a hind branch.

VOL
27
194

### d. The muscles of the body.

In all the forms possessing appendages and which have retained segmentation of the body the musculature in the main is very uniform. It consists of dorsal extensors and ventral flexors of the body. Each pair of appendages has a special musculature of its own represented by anterior and posterior bundles that form an angle in converging at the base of the limb.

Such is the structural type of the musculature in all Synagogidae with the exception of the females of Ascothorax ophioctenis in which, owing to the fixed position of their body, the musculature in the segments is somewhat reduced though it retains nevertheless its typical localisation.

As regards the Lauridae a description of the musculature exists only for Laura gerardiae. According to KNIPOWITSCH (1892) the distribution of the muscular strands is similar to that in the Synagogidae.

The Dendrogasteridae (Dendrogaster and Myriocladus)—owing to the reduction of the body and of the appendages have lost their segmentary musculature as well as the muscles of their thoracic limbs. (KNIPOWITSCH 1892, LE ROI 1907 and OKADA 1925). The adductor muscle of the valves is strongly developed only in the forms with a distinctly segmented body and more or less movable valves. This muscle lies always between the interior part of the mid-gut and the abdominal nervous system: i.e. ventrad of the gut.

In the genera: Synagoga (NORMAN 1912, OKADA 1926), Ascothorax (DJAKONOV 1914, STEPHENSEN 1936 and my proper findings—see chapter IV of this paper), Petrarca (FOWLER 1890) Laura (LACAZE-DUTHIERS 1883 and KNIPOWITSCH 1892), Baccalaureus (BROCH 1929, JOSII 1931 b, PYEFINCH 1934 and 1936) this muscle is well developed and presents no traces of rud-

imentation. In the genus Dendrogaster (KNIPOWITSCH 1892), it shows a beginning of rudimentation, and in the genus Myriocladus (LE ROI 1907 and JOSHI 1931 a) the muscle has entirely disappeared. OKADA (1925) gives a reproduction of this muscle but makes no mention of it in his description of the new genus Myriocladus.

The above data refer only to the female individuals of the two last named genera. The Dendrogasteridae males possess distinct valves and a well developed adductor muscle (KNIPOWITSCH 1892, and my own findings on the males of the genus Myriocladus). In the females of Dendrogasteridae the muscles of the mantle are highly developed—this may be inferred from the descriptions of the movements produced by the "arms" in D. astericola (KNIPOWITSCH 1892) and in Myriocladus (JOSHI 1931 a).

In many instances mention is made of the existence of striation in the musculature (KNIPOWITSCH 1892, LE ROI 1907, JOSHI 1931 a, PYEFINCH 1936 and others). The structure of the musculature in Ascothorax ophioctenis (see chapter IV) indicates that this is one of the but slightly modified Ascothoracida forms.

VOL. 27 1946

### e. The connective tissue and the lacunary system.

The connective tissue envelopes all the internal organs and adhers to the hypodermal layer on which the chitin reposes. The body cavity is filled with a connective tissue mass forming a more or less close network of lacunes. The lacunes are a substitute of the absent vascular system. The vascular system in Laura gerardiae described by LACAZE-DUTHIERS (1883) has been found on closer inspection—carried out by KNIPOWITSCH—to be a system of lacunes (KNIPOWITSCH 1892). In the works of other authors the existense of a lacunary system is only mentioned (OKADA 1925, JOSHI 1931 a and b, PYEFINCH 1936), but nothing is said of the topography of the lacunes. The lacunary liquid contains variously shaped amoeboid cells.

### f. The excretory system.

In the Ascothoracida, as in all Entomostraca the excretory system is represented by the maxillary glands; these glands in various Ascothoracida are not uniform in their structure.

According to literary data it is in the Lauridae that these glands possess the most complex structure. Thus in Laura Knipowitsch (1892) described two pairs of coelomic cavities opening outward by way of one common duct. The cavities are connected with each other by a short duct opening into the posterior cavity by a funnel, which cavity KNIPOWITSCH homologises with the coelom.

The other forms of Ascothoracida possess no more than one pair of the sac-like cavities of the maxillary gland. In Synagoga metacrinicola the sac-like

portion forms three lobe-like protrusions; OKADA (1926) considers this portion to be similar with the cavities described in Laura gerardiae. In the genus Baccalaureus the cavities of the maxillary glands are somewhat simplified in their structure. Thus in B. japonicus sacs (JOSHI 1931 b) have been described, while in B. hexapus Pyefinch (1936) has found simple sacs possessing no lobulated protrusions (PYEFINCH 1936). In the Dendrogasteridae (KNIPOWITSCH 1892, LE ROI 1907, OKADA 1925) the excretory system is represented by simple sac-like cavities and a narrow duct opening at the base of the maxillae. The excretory system in Ascothorax ophioctenis has about the same structure (see chapter IV).

The change to cavital parasitism and a certain degree of degradation of the organism due to the new mode of life influences also the structure of the excretory system. The fact that in Synagoga and Laura the excretory organs are similar in structure and that in Ascothorax and Baccalaureus hexapus these organs have undergone about the same degree of degradations may be considered as corroborating the conclusion that the Synagogidae and Lauridae had a common ancestor. The Dendrogasteridae represent a further step towards simplification. In regard of the degree of its development the structure of the excretory system in Ascothorax (the most highly modified genus in the family Synagogidae) is intermediate between the structure of the excretory system of the Dendrogasteridae and that of the genus Synagoga.

VOL
27
194

### g. The reproductive system.

All the Ascothoracida are dioecious; Petrarca bathyactidis alone is an exception—it is a hermaphrodite.

The males are known in many Ascothoracida forms. However detailed descriptions of the male reproductive organs are but few. Such descriptions have been given by JOSHI (1931 b) for Baccalaureus japonicus and by KNIPOWITSCH (1892) who has described the males of Dendrogaster astericola.

In other papers the authors either only mention having found the males, or they give a rough sketch of the organisation of the males, frequently restricting themselves to description of the external anatomy. Indications of this sort may be found in the papers of LE ROI (1907), NORMAN (1912), KRÜGER (1920), DJAKONOV (1914), OKADA (1926), STEPHENSEN (1935), BRATTSTRÖM (1936 b).

In the Baccalaureus japonicus males the unpaired germinative gland is represented by a central mass which sends off lateral lobes into the mantle valves. From this central mass the vasa defferentia also take their beginning; they open into a large penis which lies on the ventral side of the first abdominal segment (JOSHI 1931).

It is of interest to note that in the Baccalaureus males in the inferior edges of the valves, JOSHI found cells presenting an analogy to maturing

oocytes. In view of this the opinion was emitted that the males are possibly hermaphroditic.

Such instances, when the gonad of the male contains at the same time a primordium of the female gonad are not infrequent, and have been found even among other animal types (see MEISENHEIMER 1925).

In Dendrogaster astericola the testes are described as a cellular mass localised in the anterior portion of the body and penetrating into the sac like prolongations of the posterior portions of the mantle valves. KNIPOWITSCH supposed them to be of testicular nature but gave no distinct answer to the question. The observations made by LE ROI (1905), KLUGGE (in litt.) on the males of Dendrogaster murmanensis, and my own as yet unpublished data obtained on the males of Myriocladus sp. sp. present definite proof of the testicular nature of these formations.

A good description exists of the male reproductive system in the hermaphrodite Petrarca bathyactidis.

In Petrarca, as in all the males mentioned above, the testes lie dorsad of the gut and in the dorsal portions of the mantle. They are well developed and are no doubt functionating. This may be concluded from the stages of spermatogenesis and the seminal ducts which arise from each lobe of the testis agree with those of Ascothorax (see chapt. IV). The seminal ducts open into the vasa deferentia which run parallel to the gut and open separately into a very large penis localised on the ventral side of the first abdominal segment (FOWLER 1890).

In the males of Ascothorax ophioctenis a male gonad alone is present (see chapt. IV).

1. *The female reproductive system in all the forms belonging to this group is uniform in its structure* so that it will suffice to give a general description of the organs, with addition of certain details. The female gonad like the male gonad, is unpaired. It lies above the mid-gut on the border line between the cephalic and the thoracic portions of the body. From the unpaired portion of the ovary lateral lobes arise; these lobes give off variously ramifying branches within the mantle valves. The degree and the character of the branching depends on the structure of the valves. As a rule the branches of the gonads run parallel to the gut diverticula.

In the unpaired portion of the ovary we find division of the germ cells while, in the lateral branches, maturation, growth and the appearance of yolk in germ cells takes place.

The oviducts arise at the base of the lateral branches and open at the base of the first pair of thoracic limbs or in the Dendrogasteridae and in Baccalaureus —at the corresponding points of their body.

The Ascothoracida possess no yolk glands—as were described by PYEFINCH

(1936) in Baccalaureus hexapus. This is clearly to be seen if careful comparison is made of the figures in PYEFINCH's paper (1936, figs. 28 and 32, pl. 39) with the microscopical picture presented by the sections made of the branches of the ovary containing mature oocytes. I was led to form these conclusions on studying in sections the ovaries of the females of Ascothorax and by comparing the figures given by PYEFINCH with the reproductions found in other authors (KNIPOWITSCH 1892 and LE ROI 1907).

The figures of the yolk glands are simply a reproduction of sections made in the extreme portion of mature oocytes. Owing to deficient fixation (and probably also to deficient staining) the structure of the oocytes has been to such an extent modified that it has proved difficult to discover the nuclei in them, and herein presumably lies the reason why PYEFINCH came to consider them as yolk glands which possess no nuclei.

If in Crustaceans such an organ were really present the generally accepted views in regard of the reproductive system in their group would have to be be radically modified, but these data are based on erroneous observation.

VOL
27
194

*2. The receptacula seminis (testis according to LACAZE-DUTHIERS and PYEFINCH, dermal glands—according to KNIPOWITSCH).*

In the females of the Ascothoracida, on the outer portions of the coxopodites of the II to V pairs of the thoracopodia lie the receptacula seminis. They are represented by more or less considerably swelled chitinized tubes inverted into the segment. They may be distinctly seen in sections and have never been known to occur outside the II to V pair of the thoracopodia. If a form possesses less than six thoracic limbs the localisation of the receptacula seminis may help to determine what limbs have been retained.

The authors differ in their opinions on the meaning of this organ. LACAZE-DUTHIERS who first observed it in Laura gerardiae saw that grains resembling spermatozoa may be pressed out of them, and considered them as testes.

KNIPOWITSCH (1892) finding in his reinvestigations of Laura no stages of spermatogensis in the body of the females of Laura concluded that these organs are some sort of dermal glands. Contrary to LACAZE-DUTHIER'S opinion, KNIPOWITSCH speaks of Laura as of a dioecious form.

JOSHI (1931) notes the resemblance of the "granules of secretion" with ripe spermia found in the vasa defferentia of the males but arrives at no definite conclusion, and leaves the question open. PYEFINCH (1934) notes in Baccalaureus maldiviensis the presence of peculiar glands in the thoracopodia. His point of view respecting these organs has been definitely studied by the author in 1936, in his description of Baccalaureus hexapus.

PYEFINCH considers them as testes; in his paper this author lays great stress on their presence and discusses the question of hermaphroditism in Baccalaureus.

Together with this he gives an exact description of the organs from an anatomical and a topographical point of view.

"The testes (writes PYEFINCH in his paper 1936) are situated at the proximal end of the appendages of the ... thoracic segments ... They open by a number of pores ... over (a) region of the appendages so that a surface mount of this part appears grid-like. Immediately below each opening is a small chamber, chitin lined into which the spermia pass before they are expelled (fig. 35, pl. 40, *l.c.*)." PYEFINCH next studied spermatogenesis; he gives a description of various stages of the maturation of the sperm. He found mono-, bi-, and multinucleate forms of spermatogonia, the latter forming the "rosette stage" (figs. 33 and 34, pl. 40, *l.c.*). It has not been possible to this author to find any stage between the rosette stage and the ripe spermia. The long filiform spermatozoa are formed in bundles and pass out arranged in this way (fig. 35, pl. 40, *l.c.*). PYEFINCH'S figures 34 and 35 (pl. 40) represent the "early and late rosette stages" of this author.

On examining my slides I found the explanation of the pictures described by PYEFINCH. As mentioned above each of the small sacs is a chitinous formation. Below the chitin lies an even hypodermal layer. The sections made of the summit and the middle of such a sac, or tubule, give each a different picture, and these agree with the different stages of spermatogenesis as described by PYEFINCH. The "early rosette stages" are found in the sections made through the summit of the sac, and, this summit being hemispherical, it follows that the hypoderm underlying the chitin also curves in the form of a hemisphere. By reason of this such section show a central nucleus, and, about it, from 4 to 6 nuclei entirely similar to those reproduced by PYEFINCH.

The "late rosettes" are the cells surrounding the nucleus which has divided giving rise to spermia (?). These late rosette stages may be found in the sections made of the distal ends or the middle of the tubules. Spermia in these tubules are certainly present but they come from the testes of the males.

Quite similar pictures were found by me on sections made of the thoracopodia of the Ascothorax females. On comparing them with the pictures presented by the spermia in the vasa deferentia of the males I arrived at the conclusion that the grains in the tubules are quite identical formations. Look as I would I could find no spermatogenesis in the females, whereas in the males secured at the same period—time—spermatogenesis was at its highest but presented no "rosette" stages. In view of this it must be concluded that PYEFINCH'S data respecting the hermaphroditism of Baccalaureus hexapus and B. maldiviensis are erroneous, especially as JOSHI (1931 b) described an indubitable male in Baccalaureus japonicus. The testes described by PYEFINCH must be considered as homologous with the receptacula seminis in the thoracopodia of the females of Ascothorax ophioctenis (see chapt. IV).

Receptacula seminis in the thoracopodia of the females are known now in such Ascothoracida which possess free swimming males (Lauridae) and internal mobile males (Ascothorax). The Dendrogasteridae have no receptacula seminis which is presumably due to the reduction of the thoracopodia.

### h. Fertilization.

The fertilization appears to be external; it occurs at the moment when the egg, leaving the oviduct passes by the base of the thoracopodia. While pressing against the thoracopodia the egg causes spermia to leave the receptacula seminis and in this way fertilization is achieved.

In the Dendrogasteridae fertilization takes place immediately in the mantle cavity into which the males give off their sperm. The strong development of the penis is probably due to the males having to introduce it into the mantle cavity of the females from outside, and so inject the sperm.

The Ascothorax males live together with the females in the bursal cavity of Ophiuroids. Being capable of moving freely about in the bursa the males, when giving off their sperm, can come quite close to the mantle aperture of the female, and, in conjunctive with this, their penis is considerably shorter.

## D. THE LARVAE.

In all Ascothoracida the embryos develop in the brood pouches of the females. The larvae hatch from the eggs at the nauplius, in some forms—in the metanauplius (Myriocladus), and even in the ascothoracid (Dendrogaster) stage.

The stages at which in Ascothoracida the larvae slip from the brood pouches vary according to the form. In the Lauridae and in the genus Synagoga (?) they slip out at the nauplius stage (Lacaze-Duthiers 1883, Knipowitsch 1892, Okada 1926, Josii 1931 b, Pyefinch 1934, 1936); in the Dendrogasteridae and in the genus Ascothorax—at the ascothoracid stage (Knipowitsch 1892, Djakonov 1914, Fischer 1930, Brattsrtöm 1936 and my own findings—see chapt. IV of the present paper). Okada (1925) indicates erroneously that in Myriocladus the larvae leave the brood pouch at the metanauplius stage. The examination of the material which A. V. Ivanov had collected and put kindly at my disposal (I owe A. V. Ivanov my grateful acknowledgement for this) showed Myriocladus sp. sp. to contain larvae in the ascothoracid stage. The conclusion is that in the genus Myriocladus the development in the brood pouches continues up to the ascothoracid stage, at which stage the larvae slip out.



VOL
27
194

### a. The Nauplius stage.

On comparing the various nauplius stages in the Ascothoracida the considerable differences between the larvae which leave the brood pouch in this stage (Lauridae) and such as continue their development within the brood pouches up to more advanced stages (Dendrogasteridae, Ascothorax) were noted. The first possess well developed appendages abounding in additional formations such as numerous long natatory spines and various processess and dents. The larvae are, besides, much less rich in yolk than the nauplii belonging to the other group; their dorsal carapax is less distended as compared with the latter. The strongly distended carapax of the nauplii of the Dendrogastridae and of Ascothorax is filled with yolk. Owing to this their form is nearly spherical and their appendages, together with the additional structure of the limbs, are much less developed; broad spines are entirely absent; the bristles are in part rudimentary while the longer ones are correspondingly shorter than in the nauplii of the first group. A characteristic feature common to all the nauplii is the absence of the nauplius eye and of the lateral spines in the fore part of the cephalic carapax.

From a comparison of the nauplii of these two groups with each other it may be concluded that in more ancient forms, such as the Lauridae as well as in the more recent forms which, owing to their ectoparasitic mode of life, have retained a primitive organization (Synagoga) the nauplius stage is an active larval stage. On the setting in of cavital parasitism the incubatory period increases and the free larval stages are curtailed.

In such forms the nauplii—while retaining their general aspect are embryonic in character. This finds itself expressed in that they still possess a large amount of yolk, and that the appendages together with their additional structures are feebly developed. It is in the nauplii of Myriocladus (Josii 1931 a, Okada 1925) that this process attains its highest degree. Knipowitsch found no nauplius stages in Dendrogaster; this author, basing on the material at his disposal established that out of the egg an ascothoracid (cypris-like according to Knipowitsch) larva hatches, consequently in this form the number of larval stages is curtailed to one—the terminal ascothoracid stage. The same has been noted by Klugge for Dendrogaster murmanensis Klugge. Brattström (1936) is of opinion that this decrease in the larval stages in Dendrogaster astericola is due to the specific hydrological conditions which exist in the arctic seas. However, in Ascothorax ophioctenis—also an arctic form,—no abbreviation of the larval period has been noted—in this form it is nauplius larvae that hatch from the eggs. Most probably it is an adaptive peculiarity of the genus Dendrogaster connected with the endoparasitic mode of life of the genus.

### b. The Ascothoracid larvae.

The ascothoracid larvae (cypris-like larvae of other authors) are known at present in all the genera of the fam. Dendrogastridae and in the genus Ascothorax. They were described: in Ascothorax by DJAKONOV (1914), in Dendrogaster by KNIPOWITSCH (1892) and FISCHER (1930), in Ulophysema by BRATTSTRÖM (1936) *and* for Myriocladus evidence of the presence of such larvae was obtained from the materials at my disposal.

In the Lauridae, contrary to the indications given by LACAZE-DUTHIERS (1883) and by PYEFINCH (1936), ascothoracid- (cypris-) like larvae are unknown. What these authors considered to be larvae were the males, described in detail by JOSII (1931 b).[1] In the Lauridae the ascothoracid stage is presumably represented by a free swimming larva. The larva, described by MCMURICH (1917) as a larva of Ascothoracida, belongs apparently to the fam. Dendrogasteridae. I cannot however give a decisive judgement on this point as MCMURICH's original paper is unknown to me and I cited it after BRATTSTRÖM (1936) and STEPHENSEN (1935).

The larvae of Dendrogaster and Ulophysema possess according to KNIPOWITSCH (1892) and BRATTSTRÖM (1936), a distinctly segmented body in which the same three portions may be recognised as in Ascothorax ophioctenis. I arrived at the same conclusions when making a preliminary examination of the larvae of Myriocladus sp. sp.

The larvae of Dendrogaster differ from those of Ascothorax in that they possess fewer thoracic appendages. There are 5 pairs of them instead of six as in Ascothorax. If we are to judge only by the data existing in literature—the abdominal segments in the ascothoracid larvae of Dendrogasteridae are present in smaller numbers than in the larvae of Ascothorax—4 against 5 segments, without counting the furca. My own observations made on the ascothoracid larvae of Myriocladus and a detailed examination of the figures given by KNIPOWITSCH (1892) and by BRATTSTRÖM (1936) lead us to infer that the descriptions of the abdominal portion given by these authors are erroneous. Both authors are of opinion that the reduction occurred in the VI pair of the thoracopodia and that the sixth thoracic segment deprived of limbs bears on its ventral side a conical penis-like protrusion; it is reproduced in the papers of BRATTSTRÖM (1936) and of KNIPOWITSCH (1892). The last named author states in his thesis (p. 24) "five thoracic segments bear thoracopodia while the sixth segment possesses an additional formation corresponding to a penis. Next comes a highly developed abdomen composed of four segments and the furca". BRATTSTRÖM's account is fairly similar. However I can not accept this point of view owing to the comparison I made of

[1] BRATTSTRÖM in 1936 has given an account of another male belonging to the genus Baccalaureus B. argalicornis Brattström (1936 b).

these larvae with the larvae of Ascothorax. As may be seen from the above the last named possess six pairs of thoracopodia and 5 abdominal segments of which the first bears a small conical protrusion corresponding to the penis of the adult males. Characteristic for all known Ascothoracida is the presence of the penis situated on the first abdominal segment, and there can be no reason to ascribe to the ascothoracid larvae and the males of Dendrogasteridae a localisation of the organ in the thoracic region. Besides in the larvae of Dendrogasteridae it is not the sixth but the first thoracic segment that has lost its appendages by reduction, or more exactly—by atrophy. This point of view is supported by the fact that in Ascothorax the first pair of thoracopodia is rudimentary even in larvae.

Basing on the above the ascothoracid larvae of Dendrogasteridae must be considered to possess not four but five abdominal segments as—in analogy with what has been found in the Ascothoracida—the segment bearing the primordium of the penis must be designated as the first abdominal segment. This finds confirmation in the fact that five segments have been noted in the abdomen of the females of Ulophysema (Brattström 1936) as well as in the males of Dendrogaster astericola (Knipowitsch 1892, figs. 16 and 17, pl. II) and of Myriocladus sp. sp.

A characteristic feature common to all larvae in the ascothoracid stage is the bivalvate mantle with its short dorsal suture, the adductor muscle of the valves, shear-like antennulae, mouth pieces of the piercing and sucking type, and a well developed abdomen composed of five segments and bearing a natatory furca.

Finally it is to be noted that, although the reduction and alteration of a number of organs has occurred in the adult, the ascothoracid larvae retain the structural plan common to the group (the only exception is the reduction of the first pair of thoracopodia in the Dendrogasteridae). It follows that even in the most strongly modified forms in which segmentation had entirely disappeared the ascothoracid larvae reproduce in many of their characteristic features the structure of the primitive forms of Ascothoracida. This stands out clearly when larvae (see chapt. IV) are compared with the adult ectoparasitic Synagogidae and the males of Baccalaureus.

## E. THE RELATION OF PARASITE TO HOST.

Among the Ascothoracida both ectoparasitic and endoparasitic forms occur. Typical ectoparasites are both Synagoga species. Of these, Synagoga mira lives in the coral Antipathes larix Ellis, and has the ability of changing its place on the host to which it is but temporarily attached. Norman (1912) considers them to be ectoparasites. In my opinion Synagoga mira is rather to

be considered as a stenothropic predaceous form or, which is also possible, as a temporary parasite.

A similar stenotrophic predaceous mode of life is the "commensalism" on hydroids of Amphipoda Caprellidae in which complex morphological changes appear.

The data presented above show that Crustacea frequently occur together with the Coelenterata which they use as food. The probability is that the Ascothoracida ancestors had in a similar manner adapted themselves to corals which they used for nourishment and parasites of which they became (Lauridae —see further below). Another species—Synagoga metacrinicola parasitates on the inside of the disk of Metacrinus rotundus Carpenter. According to the account given by OKADA (1926) the parasite never changes its place. This is proved by the depression produced by the Crustacean on the body of the host. However, judging by the structure of the limbs it may be inferred that the ability of a change of place has not been entirely lost by the animal. This parasite feeds on the liquids of the host's body by piercing the tissues with its pointed oral appendages.

Ascothorax ophioctenis—the third form belonging to this family—has grown (or more exactly is in the act of growing) endoparasitic. While living in the bursal cavities of Ophiocten sericeum Forb, it is at the same issue, on the one hand, closely attached to the host, and on the other hand is connected with the outher medium by means of the wide bursal apertures of the host.

The fam. Dendrogasteridae is represented by typical endoparasitic forms. Of these forms—Ulophysema öresundense parasitates in the body cavity of Spatangidae (Echinocardium cordatum Pennant). It still retains its connection with the outer medium by boring holes in the carapax of the sea urchin near its anal field. The parasite feeds on the gonads of its host. The gonads lying in close vicinity to the host either do not reach their full development, or complete castration occurs (BRATTSTRÖM 1936). In 1937 BRATTSTRÖM gave a description of another form belonging to this genus—U. pourtalesiae from the body cavity of the Spatangid Pourtalesia jeffreisi W. Thompson from the Greenland Sea. These parasites also bore holes in the exoskeleton of their host.

The genera Dendrogaster and Myriocladus parasitate in the body cavity of various star fishes. The character of their way of nourishment is so far not known exactly; they probably feed on the coelomic liquid of the host.

Certain authors have cited instances of an inhibition in the development of the gonads in the interradii of the starfishes inhabited by the parasite. (FISCHER 1930, JOSII 1931 a, KORSCHELT 1933). Petrarca bathyactidis feeds on and lives in the gastrovascular system of the single coral Bathyactis symmetrica.

Quite peculiar is the parasitism in the Lauridae. The females of various Lauridae parasitate below the sarcolemma in corals (Antipatharia, Gorgonaria

and Zoantharia). They produce on the colonies of their hosts large gal-like swellings. The way of taking up food in the females of the Lauridae is so far not distinctly known. The body of the animal lying deep within its mantle cavity an active sucking of the host's tissues is scarcely possible. The suggestion that nurture is taken up by the surface of the mantle has been corroborated for Laura gerardiae only—LACAZE-DUTHIERS (1883) and KNIPOWITSCH (1892).

The question of the way of feeding of Baccalaureus hexapus is likewise unsolved; it is known only that food particles have been found in the gut. PYEFINCH (1936) makes various suggestions but gives, however, no definite answer to the question he has put forth. In my opinion the most probable hypothesis is that the food taken up by the coral comes to be contained in the mantle cavity of the parasite. As regards the two other hypotheses, namely the detaching of portions of the host's tissues by the spines belonging to the mantle, and the osmotic way of taking up food these must be experimentally proved on live objects. Such is also PYEFINCH's opinion. The males belonging to the fam. Lauridae (Baccalaureus japonicus, B. argalicornis and those of Laura gerardiae) live as ectoparasites on the same corals in which the females of these forms are endoparasites (LACAZE-DUTHIERS 1883, JOSII 1931 b, BRATTSTRÖM 1936 b). They feed presumably on the tissues of the host as their well developed mouth pieces gives reason to infer.

In comparing the various modes of parasitism of the different groups of Ascothoracida we are led to conclude that the Lauridae and Synagogidae are diverging branches independent of each other, originated from a common ancestor. The most ancient is the parasitism on corals. Primarily it must have had the aspect of a stenotroph predaceous mode of life or of a temporary parasitism. At the present day such a mode of life has been retained by Synagoga mira and the males of Lauridae. In the course of evolution the adaptation to the parasite mode of life went two different ways: 1) in the direction of a change to endoparasitism in corals—Petrarca and the females of the Lauridae, whereas the males of Lauridae have retained the ancestral character of parasitism, 2) adaptation to a life on and in the body of Echinodermata—Synagogidae. (The ectoparasitism in Crinoidea of Synagoga metacrinicola and the form of parasitism, tending towards endoparasitism, of Ascothorax ophioctenis living in the bursae of Ophiuroids.)

Next we find a transition to parasitism within the body cavity of Echinoidea and Asteroidea. The evolution of the family Dendrogasteridae may be considered as a result of adaptation to this mode of life.

## F. THE RELATION BETWEEN THE SEXES.

All Ascothoracida with the exception of Petrarca bathyactidis are dioecious and most of the forms are characterised by a distinct sexual dimorphism. As in many cases no exact data exist it is difficult to establish the numeric rate existing between males and females.

We shall give here in a summarized form all that is known in this respect. —In the genus Synagoga (NORMAN 1912 and OKADA 1926) sexual dimorphism is not sharply outlined, the males differing from the females by the development of the penis and the absence of brood pouches. Of the mode of life nothing is known. Ascothorax possesses dwarf males (DJAKONOV 1914, STEPHENSEN 1935 and chapter IV of the present work). These males together with the females, parasitate in the bursae of Ophiocten sericeum and take up nourishment in the same way as the females.

In the Lauridae ectoparasitic males occur (LACAZE-DUTHIERS 1883, BRATTSTRÖM 1936 b and JOSII 1931 b) they may be sometimes found on the corals near the mantle cavity of the females. Numeric data are absent. In regard of the Dendrogasteridae (Dendrogaster and Myriocladus) it is known only that males had been found (KNIPOWITSCH 1892, LE ROI 1905—1907, KLUGGE in litt., OKADA 1925). According to my own observations several males occur in the mantle cavity of the female forms of Myriocladus sp. sp.—as much as five males have been found in one female.

In one instance only (Synagoga mira) the males and females are nearly undistinguishable from each other. In the other instance sexual dimorphismus is very characteristic, and most forms possess dwarf males. The females in such forms are usually larger and are more strongly modified than the males. Characteristic for all the males is their more primitive structure as compared with that of the females of the same species. According to their mode of life the males may be classified as follows: 1) ectoparasitic forms standing in no constant relation to a given female—"*free males*" (Lauridae), and 2) males parasitating together with the females (Ascothorax and Dendrogasteridae). This group may in its turn be classified in two: a) males parasitating outside of the body of the female—.I propose to designate them as "ectandric forms" males (of the Ascothorax type) and b) males parasitating (living) in the mantle cavity of the females—"endandric forms" (Dendrogasteridae type).

As regards the females which become endoparasitic the extent in which they lose their capacity for moving freely about is the greater the deeper they are buried within the body of the host. The appendages, and with them also the segmentation of the body, disappear, while the gonads and the brood pouches become strongly developed; by reasons of this the mantle valves come to extend considerably. In the males likewise, as in the females, the valves grow



VOL
27
194

larger (owing to the testes)—a circumstance probably to be accounted for by the number of embryos increasing with the change to the endoparasitic mode of life. Thus we find that the reduction of mobility and the increase in size of the mantle in the Ascothoracida is characteristic for both sexes.

On comparing the relations between the sexes in various forms evidence is obtained that these relations went different ways in their development. Primarily the males and females were similar in shape and were equal in the degree of their mobility. Subsequently, with the setting in of the parasitic mode of life sexual dimorphism makes its appearance, and the males frequently change into dwarf forms. The adaptation of the males went two different ways. 1) When occurring in one direction forms possessing "free males"[1] were the result of evolution. They retained the ectoparasitic mode of life, a primitive structure and the ability to a change of place. The females of these forms have become endoparasitic (Lauridae). 2) On the evolution taking another direction forms appeared in which both sexes became endoparasitic; these are synandrobionts[2] (Ascothorax and Dendrogasteridae). The "ectandric" must have been the earlier forms (Ascothorax) while the "endandric" appeared later (Dendrogasteridae).

The question of the origin of hermaphroditism in Petrarca is difficult to solve. It may be a secondary phenomenon as: 1) in the organisation in Petrarca various modifications have occured indicating that Petrarca has diverged from the primitive forms. There are a reduction of the thoracopodia which take on the form of appendages composed of but a single joint, the rudimentation of the abdominal portion, and complete disappearance of the furca. Consequently Petrarca cannot be considered as a primitive form in our group. 2) The primitive forms of Ascothoracida are dioecious and so is the majority of the forms belonging to this group. 3) The Lauridae (males of Baccalaureus japonicus) possess in the lower portions of their valves accumulations of cells resembling oocytes. In view of this Josii (1931 b) concludes that a tendency towards hermaphroditism is proper to the Lauridae. In Petrarca bathyactidis the germinative glands are similarly localised.

However the Lauridae are primarily dioecious and the tendency towards hermaphroditism must have appeared in them is a secondary phenomenon.

[1] I propose the following special classification for the various biological groups of the dwarf males 1) "free males" and for the corresponding forms "atelandrobiontic forms" (produced from the greek words: atelos—free and endros—male (man). The females in such forms lead an attached or parasitic mode of life, whereas the males even when parasitic are capable of moving freely about and are presumably capable of going over to another female.

[2] As synandrobionts are designated such organisms in which males and females live together during all their life. The male does not move about, he is, one might say, attached to a certain female. In this group two categories of forms may be distinguished: 1) *ectandric* forms the males live together with the females and never leave them. (When parasitic they inhabit the same organ of the host.) 2) *endandric*—the males become parasitic or come to live in the cavities of the female. To the first category belongs Ascothorax ophioctenis; to the second the males of Dendrogaster and Myriocladus.

When comparison is made of various anatomical peculiarities proper to the Lauridae and the Petrarcidae the two groups are found to have much in common. This entitles us to suggest that the Petrarcidae and the Lauridae originated from a common ancestor and this is a further proof in favour of my suggestion.

We come now to discuss the question of the secondary dioeciousness in the Ascothoracida (KNIPOWITSCH 1892, pp. 88—89, of his monography). KNIPOWITSCH in his conclusions bases on the comparison of Petrarca which is insufficiently known with Laura and Dendrogaster. This author mentions the presence of a vestigial penis in the ascothoracid larva (cypris larva according to KNIPOWITSCH) of Dendrogaster as corroborating his point of view.

This proof however seems but insufficiently conclusive. The presence of a vestigial penis in the Synagogidae and Lauridae female—both in larvae as in the adult—(in the Lauridae females it is especially distinct) proves rather that these forms are sexually indifferent than that the dioecious forms are descended from hermaphroditic forms.

Basing on the sex rate, we have reason to suppose that in some cases there is metagamic determination of the sex. This form of determination of sex has been described for Cirripedians closely related to the Ascothoracida (KÜHNERT 1934). Presumably of all larvae that have penetrated into one host the first grows to be a female, while all the others metamorphose into males—as it is known for Alcippe lampas Hancock (KÜHNERT 1934). This, in my opinion, is so far the only possible explanation of the presence of a rudimentary penis in seemingly indifferent Ascothoracid larvae.

The other—no less plausible—hypothesis is the one suggested by LE ROI in his unpublished work on Dendrogaster repertus (cited after KRÜGER 1920) of the parthenogenetic origin of the Dendrogasteridae males, but KRÜGER gives no detailed explanations. G. A. KLUGGE[1] likewise suggests the same explanation with regard to the question of the origin of the males of Dendrogaster murmanensis Klugge (in litt.). KLUGGE's conclusions are based on the observations made on young D. murmanensis females, within the mantle cavity of which he found several ascothoracid larvae and numerous intermediate forms showing the metamorphosis of such larvae into males. In some instances KLUGGE found over 20 young males in one female. These phenomenona occur in the summer season, the next period of propagation falls in the winter season, when in the mantle cavity of the female ripe males are already contained. In view of this KLUGGE concludes that the D. murmanensis females lay eggs twice a year. From the first (summer) batch parthenogenetic males are developed, whereas the winter eggs are fertilised, and from these larvae capable of infesting

[1] I tender my thanks to G. A. KLUGGE for the permission to cite in these pages his as yet unpublished data.



VOL
27
194

the host are produced—such larvae metamorphose into females. KLUGGE mentions—as confirming his point of view—the circumstance that in some instances the star fish is found to contain numerous females of various age (size, whereas in the case of a metagamic determination of sex all the younger larvae ought to have metamorphosed into males—which as a matter of fact does not take place. Given that KLUGGE's suggestion is the right one — in that case the meaning of the exuvia that KNIPOWITSCH found in the mantle cavity of Dendrogaster astericola females may easily be explained—they are thrown off by the parthenogenetic larvae when changing into males — and KNIPOWITSCH states having found males.

For the final solving of the question of parthogenetic and metagamic males further detailed cytological investigations are necessary; the points of view here emitted may be considered only as hypotheses.

VOL. 27 1946

## G. GEOGRAPHICAL DISTRIBUTION.

The Ascothoracida occur in all oceanic basins of the northern hemisphere, and in their distribution—though the species are but few in number—certain regularities may be noted. In the first place mention must be made of a distinct tendency towards an amphiboreal distribution (BERG 1918 and 1934) of species belonging to one genus, and respectively of genera within the families. Into this zoogeographical category belong the species of the genus Synagoga of which Synagoga mira—the most primitive form in this genus—is found in the Mediterranean (Golf of Naples) and Synagoga metacrinicola—in the Japanese Sea. Not less interesting is the distribution of the species belonging to the genus Dendrogaster; two of the species occur; the one in the Kola Bay (Barents Sea)—Dendrogaster murmanensis Klugge, and in the White Sea—Dendrogaster astericola while the third—Dendrogaster arcticus Korschelt (Fischer)—lives in the Behring Sea (FISCHER 1930).

As regards the distribution of the genera belonging to distinct families, it may be said that they all are amphiboreal—the Petrarcidae alone excepted. Of this last named family nothing may be said so far, as it is represented by but one species—Petrarca bathyactidis. Of the family Synagogidae two genera—Synagoga and Ascothorax occur in the Atlantic Basin, while in the Pacific Basin the genus Synagoga alone has been found. Equally amphiboreal is the distribution of the Lauridae. The genus Laura—the most primitive in this family—has been found in the Mediterranean (off the Algiers coast) and Baccalaureus—another genus with a more complicated organisation occurring in the Indo-Pacific Basin. The most modified forms in this genus—Baccalaurues maldivensis Pyefinch and Baccalaureus hexapus Pyefinch—live in the Indian Ocean, the most primitive—Baccalaureus japonicus Broch—in

the Japanese Sea.[1] Of still greater interest is the distribution of the Dendrogasteridae. Three genera of this family inhabit the Atlantic Basin. Two of these—Ulophysema and Dendrogaster—occur in the North Atlantic and another genus—Myriocladus was found in the South Atlantic off the Cape of Good Hope. The home of the last named form, however, seems to be the Indian Ocean. In the Indo-Pacific Basin two genera only are known so far: Dendrogaster from the Behring Sea and Myriocladus which is widely distributed over an area extending from the Philippines to the Behring Sea. The genus includes besides a bipolar form—Myriocladus arborescens Le Roi—as it has likewise been secured in the southern hemisphere. The most primitive genera of this family are Ulophysema and Dendrogaster, the most altered form is Myriocladus.

The zonal distribution of the Ascothoracida brings into evidence another widely occurring regularity consisting in that the closer to the equator the larger is the number of the species. Thus we know of only three arctic species—Ascothorax ophioctenis Djakonov, Dendrogaster astericola Knipowitsch and Dendrogaster arcticus Korschelt (Fischer). Next, there are nine boreal species —Synagoga mira Norman, Synagoga metacrinicola Okada, Laura gerardiae Lacaze-Duthiers, Baccalaureus japonicus Broch, Ulophysema öresundense Brattström, Ulophysema pourtalesiae Brattström, Myriocladus arbusculus Fischer, Myriocladus astropectinis Josii, Myriocladus Okadai Josii. Of tropical species five only are known at present—Petrarca bathyactidis Fowler, Baccalaureus maldivensis Pyefinch, Baccalaureus hexapus Pyefinch, Baccalaureus argalicornis Brattström and Myriocladus ludwigi Le Roi. The data here presented are summarised in table III. As the material at our disposal is by far not numerous enough, it is impossible to draw any definite conclusions regarding the distribution and the centres of species formation.

## H. THE PHYLOGENY OF THE ASCOTHORACIDA.

We shall close the comparison here given by a phylogenetic survey and a discussion of the relationship between the separate forms of the Ascothoracida. The morphological and biological parallels contained in the present chapter clearly indicate that the Ascothoracida represent a distinct group their larvae and the adult formes possessing a common structural plan.

[1] Baccalaureus argalicornis Brattström (1936 b), was found off the Madagascar coast, Indian Ocean.
Baccalaureus torrensis Pyefinch (1937), was found in the Torres Strait.
Baccalaureus disparcaudatus Pyefinch (1939), Zansibar area.
Baccalaureus verrucosus Pyefinch (1939), Zansibar area.
Baccalaureus japonicus Broch—Pyefinch 1939, Zansibar area.
Baccalaureus digitatus Pyefinch 1939, Gulf of Aden.



VOL
27
194

TABLE III.

The distribution of the Ascothoracida.

| Ascothoracida | Host | Location of the parasite | Secured in | Males | Described by whom and when |
|---|---|---|---|---|---|
| Synagoga mira Nrm. | Antipathes larix Ell. | Ectoparasite or predaceous form | Golf of Naples | Isomorphic with females | NORMAN 1887—1912 |
| S. metacrinicola Ok. | Metacrinus rotondus | Constant ectoparasite | Japanese Sea | „ | OKADA 1926 |
| Ascothorax ophioctenis Dj. | Ophiocten sericeum | Endoparasite in the bursae | Barents Sea | Dwarf ectomales | DJAKONOV 1914 |
| „ | „ | „ | Greenland Sea North Atlantic | „ | STEPHENSEN 1935 |
| „ | „ | „ | Kara Sea | „ | My proper collection |
| Ulophysema öresundense Br. | Echinocardium cardatum | Body cavity | The Sound (Öresund) | | BRATTSTRÖM 1936 |
| U. pourtalesiae Br. | Pourtalesia jeffreysi | „ | Greenland Sea | | BRATTSTRÖM 1937 |
| Dendrogaster astericola Kn. | Echinaster (Cribrella) sanguinolentus Solaster ? | „ | White Sea | Dwarf "endomales" | KNIPOWITSCH 1890—1892 |
| D. sp. Fischer (Arcticus Korch.) | Leptasterias groenlandica | „ | Behring Sea | ? | FISCHER 1930 (named arcticus KORSCHELT) |
| D. murmanensis Kl. n. nud. | Grossaster papposus | „ | Barents Sea | Dwarf "endomales" | KLUGGE 1910 |
| „ | Solaster endeca | „ | Kola Bay | „ | DERJUGIN 1915 |
| Myriocladus arborescens Le Roi | Dipsicaster schleideni | „ | South Atlantic Ocean | Dwarf males | LE ROI 1905 (1907) |
| M. Okadai Josii (s. arborescens Ok.) | Asterias calamaria | „ | Japanese Sea | ? | JOSII 1931 a |
| M. astropectinis Josii | Astropecten polydentus | „ | „ | ? | JOSII 1931 a |
| M. Ludwigi Le Roi | Echinaster fallax | „ | Pacific Ocean (Philippins) | ? | LE ROI 1905—1907 |
| „ | Certonardoa semiregularis | „ | Japanese Sea | ? | JOSII 1931 a |

TABLE III.

The distribution of the Ascothoracida. (Continuation.)

| Ascothoracida | Host | Location of the parasite | Secured in | Males | Described by whom and when |
|---|---|---|---|---|---|
| Myriocladus arbusculus Fi. | Hippasteria californica | Body cavity | Pacific Ocean | ? | FISCHER 1911 |
| „ | Poraniopsis inflata | „ | „ | ? | |
| Petrarca bathyactidis Fowl. | Bathyactis symmetrica | Gastrovascular cavity | „ | | FOWLER 1890 |
| Laura gerardiae L-D. | Gerardia | Below the sarcolemma (epitheca) | Mediterranean | Free swimming ectoparasites of the same host | LACAZE-DUTHIERS 1883 |
| Baccalaureus japonicus Broch | Polythoa sp. | „ | Japanese Sea | ? | BROCH 1929 |
| „ | Zoanthus enidosus | „ | „ | Dwarf males free swimming ectoparasites of the same host | JOSHI 1931 a |
| „ | Plumularis haberlei | „ | | | |
| „ | Polythoa sp. | „ | | | |
| B. maldivensis Pyef. | Polythoa (Zoantharia) | „ | Ind. Ocean (Maldivian Isles) | ? | PYEFINCH 1934 |
| B. hexapus Pyef. | „ | „ | Java (Burma Ind. Ocean Marban) | ? | PYEFINCH 1936 |
| B. argalicornis Br. | „ | „ | Madagascar | Free swimming dwarf males | BRATTSTRÖM 1936 |

However, owing to the specific condition of parasitism the Ascothoracida forms differ in their evolution. In connection with this two different ways of development may be distinguished. We shall now discuss in detail these two ways of evolution.

As mentioned above in Ascothoracida the adaptation to parasitism occurred in two distinct directions (fig. 29). The evolution went one way in forms that for a long time retained the bivalvate character of the mantle which had a tendency to extend in a lateral direction. In such forms, in females as in males,



VOL 27 194

grasping antennules of the subchela and chela type came to develop in an equally high degree. These forms changed from ectoparasitism to endoparasitism in the coelom of Echinodermata. This transition was accompanied with a regression in segmentation up to a complete disappearance of segmentation and of the thoracopodia (Dendrogasteridae). In connection with the change to endoparasitism in these forms the relation between the sexes suffered a great change. The males that primarily resembled the females became dwarf males. Together with the females they began to parasitate in the body cavity of the host and in some cases they parasitated in the mantle cavity of the females. Together with the setting in of endoparasitism in these forms the incubation period grew to be of longer duration while the metamorphosis was abridged. A series of forms changing in the direction described belongs to the families Synagogidae and Dendrogasteridae (fig. 29). The most primitive among them is Synagoga mira, a predaceous form or a temporary parasite of the corals Antipatharia. A somewhat altered form is Synagoga metacrinicola—a constant ectoparasite of the Crinoidea. The greatest degradation in the family Synagogidae is found in Ascothorax ophioctenis Djakonov. A. ophioctenis is to a certain extent intermittent between this family and the Dendrogasteridae, as in it changes make their appearance that come to be fully expressed in the last named group, these are: progressive development of the mantle in the females, a tendency to a reduction of the thoracopodia, and appearance of dwarf males. The Dendrogasteridae are represented by highly degraded forms; they are all parasites of the coelom of the Echinodermata. The most primitive is the genus Ulophysema,—it has retained segmentation of the body and the rudiments of the thoracic limbs. The two other genera (Dendrogaster and

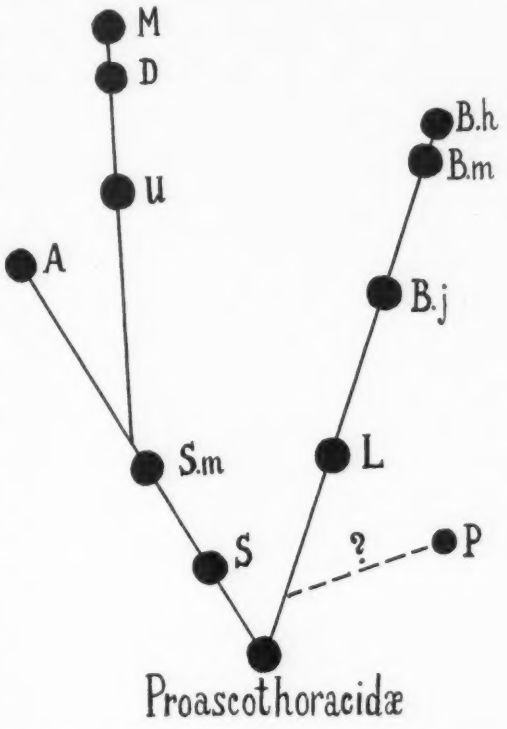



Fig. 29. Phylogenetical relations in the order Ascothoracida. *S*—Synagoga mira; *Sm*—Synagoga metacrinicola; *A*—Ascothorax; *U*—Ulophysema; *D*—Dendrogaster; *M*—Myriocladus; *P*—Petrarca; *L*—Laura gerardiae; *B.j*—Bacc. japonicus; *B.m*—Bacc. maldivensis; *Bh*—Bacc. hexapus.

Myriocladus) have definitely lost the segmentation of the body as well as their thoracic limbs. At the same time the mantle in them undergoes progressive development, and that not in females alone, but also in males. The number of embryos is greatly increased, endandric relations between the sexes make their appearance.

The evolution took another direction in the forms in which, in the females a dorsoventral extension of the mantle took place (Lauridae). Their appendages became rudimentary, the oral appendages alone remained well developed. They changed to an immobile parasitism below the sarcolemma in corals. Their dwarf males belong to the "free" type. The males are mobile and have retained the primitive ectoparasitic mode of life (athelandrobiontic forms). The mantle in the males has remained bivalvate; the appendages are but slightly reduced, if at all. The antennules are of the prochela type. It is interesting to note that in the thoracic limbs the protopodite consists of three (?) joints. The incubatory period in these forms is of short duration; the larva leaves the brood pouch in the nauplius stage. These characters are proper to various forms belonging to the fam. Lauridae. The least altered is Laura gerardiae, which species possesses a simple saclike mantle and six pairs of uniramous non bifurcated thoracopodia. Next the structure of the mantle becomes more intricate.—The simple sac changes into a double sac separated along the median plane (Baccalaureus japonicus Broch). The number of thoracic limbs is reduced to four (besides the horn-like processes and pterygiae of the thoracic portion—which Josh considers to be thoracopodia). In other species of this genus each half of the mantle is coiled and the number of thoracopodia is reduced to three pairs (Baccalaureus hexapus and others, fig. 29).

As regards the Petrarcidae (Petrarca) this family closely agrees in many of its characters with the Lauridae; however, the comparison is to be made not with the females, but with the males of this family as it is with these that they more closely agree. Such is the presence of spines on the face of the mantle valves, the strongly developed penis and the location of the germinative glands (see the paragraph in this chapter treating the relation between the sexes). Moreover both forms parasitate in the gastrovascular cavity in corals. The slightly expressed segmentation of the body in the Petrarcidae, rudimentary thoracic limbs and reduction of the abdomen may be considered as a result of endoparasitism. In the Lauridae the number of abdominal segments is reduced to four; in common with the Petrarcidae they show the tendency to a reduction of the abdomen, with that difference that in the latter this tendency is more strongly expressed then in the Lauridae. The Petrarcidae might be considered as a lateral branch (fig. 29) belonging to the trunk proper in common to this family and to the Lauridae. They must have diverged from the trunk at the very beginning of the evolution of this group. At all events they may be considered as closely related to the Lauridae.



VOL
27
194

## I. THE POSITION OF ASCOTHORAX OPHIOCTENIS IN THE SYSTEM OF ASCOTHORACIDA.

As compared with the Dendrogasteridae Ascothorax is more primitive and may be put into this family because its ascothoracid larvae possesses 6 pairs of thoracic limbs and antennules composed of five joints, whereas the Dendrogasteridae have 5 pairs of thoracopadia and the antennules are composed of 4 joints. Moreover in Ascothorax the body is distinctly segmented—the adult females possess six pairs of biramous thoracopodia and a bivalvate mantle, while all these characters do not appear in the Dendrogasteridae.

By putting in parallel Ascothorax and the Lauridae the impossibility of putting Ascothorax into this family stands out most clearly, as these forms differ from each other in the following characters—the body of Ascothorax is composed of 16 segments, that of the Lauridae—of 15 segments at the utmost. The antennules in Ascothorax are equally developed in both sexes—they are rudimentary in the Lauridae females; in the males they are of the type of prochela, and not of chela as in Ascothorax. In the females of Ascothorax the mantle is extended laterally—in the Lauridae the extension takes a dorso-ventral direction. The dwarf males of Ascothorax are endoparasites—those of the Lauridae are ectoparasites. In Ascothorax the incubatory period lasts up to the ascothoracid stage—in the Lauridae it comes to a close in the nauplius stage.

Neither is it possible to consider Ascothorax as connected with the Petrarcidae family, as they differ from it in the following characteristic features: the Petrarcidae are hermaphrodites, (Ascothorax is dioecious), their antennules are composed of three joints, their abdomen is reduced and bears no furca—in Ascothorax the abdomen is normal, a furca is present and the antennules have five joints.

On comparing Ascothorax with Synagoga evidence was obtained that the form under discussion has many features in common with the genus Synagoga. These are: distinct segmentation of the body, a bivalvate mantle proper to the adult forms in both sexes; six pairs of biramous limbs—in females as in males, the gut opens outwards and the posterior edges in the labrum are not fused. However the alteration in the Ascothorax organisation that is due to the setting in of the endoparasitic mode of life does not permit to include Ascothorax in the genus Synagoga—it is distinguished from Synagoga by the following characters: Ascothorax possesses a distinctly expressed sexual dimorphism, the antennules are composed of five joints, the thoracic limbs tend to reduction, the mantle valves in females are considerably extended, the branching of the gut diverticula is more intricate (especially in females) and the incubatory period lasts up to the ascothoracid stage.

In view of the above made comparison of these differences due to secondary modification, and considering the close structural resemblance between the ascothoracid larvae of the form under discussion and the adult Synagoga, the systematical determination of Ascothorax given by DJAKONOV (1914) and STEPHENSEN (1935) must in my opinion be accepted as reflecting the true state of things. Ascothorax is a distinctly delimited and at the same time the most modified genus in the family Synagogidae Gruvel.

## VI. THE POSITION OF ASCOTHORACIDA IN THE SYSTEM OF ENTOMOSTRACA.

The Ascothoracida were classified by LACAZE-DUTHIERS (1883) as belonging into the order Cirripedia in which they formed, together with the Rhizocephala, a special group Cirripedia abortiva. Subsequently this point of view found corroboration in FOWLER's (1890) and KNIPOWITSCH's (1892) investigations. This fact is especially striking in regard of the last named author's work: KNIPOWITSCH after having made a parallel analysis of Dendrogaster astericola and Laura gerardiae and who had also embryological material at his disposal, still did not take it upon himself to make a special order of the Ascothoracida but left this group in the Cirripedia as a separate suborder, distinct from all the other Cirripedia. KNIPOWITSCH, as well as all the other, more recent authors, who have carried out investigations on Cirripedia and Ascothoracida, was influenced in his conclusions by the views emitted by KORSCHELT and HEIDER (1891) in their extensive symposium on the embryology of invertebrates. Owing to this circumstance and besides in concordance with GRUVEL's (1905) works the Ascothoracida are considered as one of the suborders of Cirripedia. Many authors are of this opinion: LE ROI (1905—1907), NORMAN (1912), DJAKONOV (1914), KRÜGER (1920, 1923 and later works). NILSON—CONTEL (1921 and later works), OKADA (1925—1926), BROCH (numerous articles, a symposium published in 1927, and his determination of the systematic position of Baccalaureus 1929), JOSII (1931 a and b), FISCHER (1911 and 1930), KORSCHELT (1934), STEPHENSEN (1935), BRATTSTRÖM (1936 a, b and 1937), and many others authors. The erroneousness of this point of view seems to me obvious. Let us try now to give a proof of it by comparing the Ascothoracida with the groups closely related to them.

### A. A COMPARISON WITH THE CIRRIPEDIA.

#### a. Adult stages.

In both groups the body is composed of three distinct portions: head, thorax, and abdomen.

In the Cirripedia the cephalic portion is greatly modifed and by means of it the animal attaches to the substratum. The cephalic portion changes into the peduncle in Lepadomorpha, into the sole in Balanomorpha or the stem in the Rhizocephala. In the Ascothoracida, on the other hand, the cephalic portion was never found to be altered, neither did it serve to attach the animal to the substratum. The attachement in this group is produced—both in the ascothoracid as in the adult stages—by means of the shear-like antennules.

In connection with the fact of the Cirripedia being attached by their cephalic portion various adaptive changes make their appearance in this group. In the cypris larvae the antennules are modified into suckers, and in the cephalic portion of the larvae and the adult forms cement glands are developed. These glands are modified dermal glands (GIESBRECHT 1912, KRÜGER 1920, 1923, BROCH 1927 and others). The secretory ducts of these glands open either at the base of the antennules (in Balanomorpha) or at their distal end, in the sucker-like portion (in Lepadomorpha). In no stage the Ascothoracida are sucker-like antennules or cement glands to be found. The cypris larvae at first attach to the substratum by means of the antennules then, very soon, the cement glands secrete their products and this substance serves to fix the larvae more solidly. Considered from the phylogenetical point of view this fact is of great importance as it indicates that the mode of attachement by means of the antennules is the primary form.

Of great moment in the Cirripedia is the change of the larval biramous thoracopodia possessing a small number of joints into cirri which bear numerous joints (secondary articulation) and serve to seize food. The appendages are not reduced, as is frequently the case in attached forms; they have modified their primary (natatory) function and come to serve as organs for the taking up of food and for the producing of a constant flow of water in the mantle cavity. The thoracic limbs in the Ascothoracida are never changed into cirri—they are either reduced (Dendrogasteridae) or function as respiratory and natatory organs (Synagoga and the males of Lauridae).

As the Cirripedia use particles of detritus for nourishment the masticating type of mouth apparatus in them has been reduced. In the Ascothoracida—even in the larvae—the oral appendages are of the pricking and sucking type. In regard of the structure of the oral apparatus the Ascothoracida and the Cirripedia have that in common, that in both groups the labrum grows into a sheath for the oral appendages.

The abdomen in the Cirripedia is reduced to an appendix composed of two or three segments, it is very slightly developed. In the cypris larvae the abdomen bears rudimentary furca which disappears in the adult.—The Ascothoracida possess a fully developed abdomen, which even in the adult bears a distinct furca (the females to Dendrogasteridae alone have no furca).

A typical peculiarity of the Cirripedia is the appearance of a skeleton

composed of calcareous plates. Their development takes place in the cypris stage in which they always appear in the form of five pairs of chitinous centres (2 scutae, 2 tergae and 1 carina). In the course of the subsequent development these plates come to be impregnated with lime. Even in forms possessing a larger number of plates the primary plates are the first to appear, while the other plates appear later; they developed in the same manner first chitinous centres come to view, and then these centres are impregnated with lime. (Broch 1919, 1927.) Herein presumably the phylogenetical sequences in the development of the skeleton is reproduced. The most ancient Lepadomorpha from the carboniferous layers of the Donets and Kusnetzk systems (described by Tschernischew 1930) possess but 5 chitinous plates. The embryological data, put in parallel with the data presented by paleontological investigations lead us to conclude that the most primitive forms possess 5 principal chitinous plates. In the recent form Ibla Darwin which is characterized by a number of primitive traits the skeletal plates are chitinous, and so are the plates in the fossile forms. In consequence the conclusion is imminent that the calcareous skeleton is phylogenetically younger. As brought into evidences by embryological studies the larger number of plates is a secondary phenomenon. While the plates grow more numerous the stem grows shorter and this results in the appearance of the skeleton of the Balanomorpha. On the transition to a fixed skeleton taking place the plates again decrease in number and their disposition becomes constant—Cataphragmus (Sowerby), Balanus (Da Costa). The fixed skeleton in which the scutae and tergae alone retain their mobility closely adhers to the substratum. The appearance of the skeleton may be considered as a secondary character connected with the attached mode of life. The Ascothoracida have no calcareous skeleton. In no stage in the life cycle may chitinous skeletogenous centres be observed.

The mantle in Cirripedia and Ascothoracida develops at first in the same manner—from the cephalic carapax, of the nauplius.

### b. Larval stages.

Later on however, in the subimaginal stages, the differenciation of the mantle diverges. In the cypris larvae the cephalic portion is greatly extended and this leads to the mantle valves coalescing on the ventral side. Owing to this the mantle aperture comes to be divided in two—an anterior aperture through which the antennules protrude and in which the cement glands open, and a posterior aperture connected with the cephalothoracic cavity. From the posterior aperture the swimming limbs and the rudimentary abdomen with its equally rudimentary furca protrude (Giesbrecht 1912, Broch 1927, Kühnert 1934). The mantle valves are coalesced all along their dorsal margin, which presumably is due to the shortening of the posterior free edges of the mantle valves,



VOL
27
194

this shortening standing in connection with the extension of the cephalic portion.

On metamorphosis setting in the larva fixes itself on the substratum with its cephalic end. The anterior mantle aperture subsequently comes to be included in the base of the peduncle (in Lepadomorpha) or in the sole (in Balanomorpha). The animal becomes attached to the substratum not only by means of its antennules in this the whole of the anterior part of the cephalic portion participates. The hind half of the larva's mantle cavity becomes the definitive mantle cavity. Correspondingly the posterior aperture becomes the definitive mantle aperture. This peculiarity in metamorphosis is proper to all Cirripedia.

In the ascothoracid larvae no extension of the cephalic portion takes place. The mantle valves hang together by a short dorsal suture only. A ventral suture never appears. If the ascothoracid larva in the course of its metamorphosis ever comes to fix on the substratum—the adherence is a temporary one and the larva attaches itself solely by means of its shear-like antennules. The only mantle cavity and the one mantle aperture proper to the larva may be put in parallel with the corresponding definitive ones. The cephalic portion is never changed to a peduncle or a sole. The mantle valves are extended posteriorly instead of anteriorly (see chapt. V).

In Cirripedia during metamorphosis an inversion i.e. a change in the body's orientation takes place. The hind part of the cephalic portion together with the rest of the body is twisted dorsally at an angle of about 90°. This takes place after the larva has fixed itself on the substratum.

In connexion with this inversion the adductor muscle of valves has come to lie dorsal to (above) the gut, exactly as it is found to be situated in the cypris larvae. The fact that this phenomenon is of a secondary nature finds its corroboration in that, in the primitive genus Ibla, the adductor muscle of valves is situated below the oesophagus which latter lies in a long loop about the muscle (DARWIN 1851). In the Ascothoracida during metamorphosis no inversion takes place. The orientation of the body in the adult is the same as in the larvae (fig. 30). The adductor muscle of valves lies always ventral to the gut.

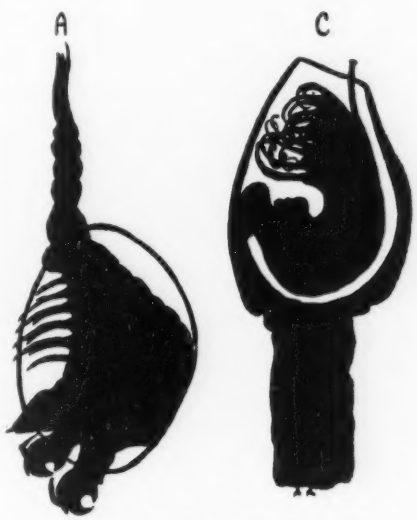



Fig. 30. Comparative orientation in Ascothorax (A) and in Cirripedia (C).

In regard of their internal organisation the Cirripedia and the Ascothoracida differ less sharply from each other, these differences appearing mostly in the details. This refers to nearly all the suborders of Cirripedia, Rhizocephala alone excepted. In the Rhizocephala owing to parasitism the internal organs have nearly completely disappeared, vestiges of the ganglion and the highly developed reproductive system alone remain. The alimentary system in Cirripedia is composed of the same portions and presents the same histological structure as the Ascothoracida (NUSSBAUM 1890, KNIPOWITSCH 1892, and other authors). The topographical differences consist in that, owing to the reduction of the abdomen the hind portion of the gut is shortened. The gut diverticula in Cirripedia tend towards reduction—in the Ascothoracida they show a progressive development.

The maxillary glands are on the whole similarly structured. There are in both cases more or less vast cavities (vestiges of the coelom) connected with the outside by ducts opening at the base of the maxillae (DEFNER 1910).

The nervous system is compact in both groups. In Lepadomorpha the ganglionary structure of the abdominal mass may still be distinguished (GRUVEL 1905).—In the Ascothoracida evidence of the abdominal mass consisting of ganglia has so far not been obtained.

The vascular system in both groups is substituted by an extended network of lacunes. There are certain differences in the structure of the reproductive system—as the Cirripedia include many hermaphroditic forms. The ovaries develop in the anterior part of the cephalic portion (the peduncle, resp. the sole) and it is only on very few forms that they extend into the mantle. The oviducts open at the base of the first pair of cirri. The testes as a rule develop only in the body proper and extend into the mantle equally in but very few forms. The paired vasa deferentia open into a penis localised on the ventral side of the first abdominal segment. In the Ascothoracida, as a rule the branches and lobes of the gonads penetrate into the mantle valves—together with the gut diverticula.

As regards the relations between the sexes—these in Cirripedia are greatly complicated by the existence of complementary males, the females are hermaphroditic (Scalpellidae, Iblidae etc.). In the Ascothoracida the relations are much more primitive. They possess sither large sized males that are outwardly similar to females, or dwarf males. Moreover all the Ascothoracida are dioecious —Petrarca bathyactides being the sole exception.

The care of the young takes the same form in both groups: the embryos develop within the mantle cavity; the Cirripedia have no special brood pouch, the incubation takes place in the very cavity between the valves. The Ascothoracida possess a special brood pouch originated from the dorsoposterior portion of the mantle valves. Owing to this their mantle extends backwards or upwards



VOL
27
194

(Dendrogasteridae and Lauridae, see chapt. V), whereas in the Cirripedia in which the cephalic portion is highly developed the mantle extends forwards.

Many striking differences are brought into evidence when larvae belonging to different suborders of Cirripedia are compared with the corresponding larval stages in the Ascothoracida. Characteristic for the Cirripedia—the Ascothoracica and Rhizocephala included—are nauplii with frontal spines (Stirnhörnchen) which bear the opening of the cephalic glands. Owing to the presence of these spines the dorsal carapax of the nauplius is of triangular shape. Its tapering hind end is frequently covered with spines and dents. All larvae—even those of parasitic forms—possess an unpaired eye. The metanauplii are very similar to the nauplii. In this stage primordia of the appendages proper to the subimaginal (cypris) stage make their appearance, and the cephalic carapax is greatly extended (DELAGE 1884, KNIPOWITSCH 1892, NILSON-CONTEL 1921, RUNNSTRÖM 1925, BROCH 1927, KÜHNERT 1934, KORSCHELT 1936 and others). The Ascothoracida nauplii are characterized by the absence of frontal spines, owing to this their carapax is of a rounded shape; at its hind edge strongly developed appendages are absent. The larvae have no unpaired eye. (LACAZE-DUTHIERS 1893, KNIPOWITSCH 1892, DJAKONOV 1914, OKADA 1925, JOSII 1913 a und b, PYEFINCH 1934 and 1936, STEPHENSEN 1935, BRATTSTRÖM 1936 and 1937.)

The subimaginal stages (the cypris and the ascothoracid stage) are distinguished by a number of characteristic features. Thus the Cirripedian cypris larvae present several distinctive features which do not exist in the ascothoracid larva. These are: strong development of the cephalic portion, ventral suture of the mantle, rudimentary abdomen and furca, sucker like antennules composed of three joints, cement glands, larval eye, skeletogenic centres that make their appearance in metamorphosis, and dorsal—in relation to the gut—localisation of the muscle adductor of valves.

The characters common to both larvae are: absence of antennae and a tendency to form an oral pyramid. In Cirripedia the pyramid includes gnawing appendages; in Ascothoracida they are of the piercing and sucking type. In both larval forms the thoracic appendages are biramous natatory limbs.

In semiparasitic and parasitic Cirrepedia (Ascothoracica and Rhizocephala), owing to reduction and various adaptations, the structural plan is greatly altered, a fact which stands out with especial distinction in various Rhizocephala. This makes it impossible to compare the adult stages of these forms with the adult stages of the Ascothoracida—and the investigator is obliged to restrict himself to *a comparison of the larval stages*. The larva having been much less influenced by the changes due to the setting in of parasitism, it may be considered that they diverged but slightly—if at all—from the typical structural plan. The evolution of the Ascothoracica, and especially of Rhizocephala indicates that these two suborders are originated from attached forms. The nauplii of the

suborders mentioned likewise possess frontal spines, cephalic glands, and strong additional structures at the hind end. Their cypris larvae, similarly to these of the other forms have a strongly developed cephalic portion, cement glands, sucker like antennules, a ventral suture in the mantle and—in common with all other Cirripedia—it is with their cephalic end that they tend to fix on the host (resp. the substratum).

In consequence, on comparing the larval stages of the parasitic Cirripedia with those of Ascothoracida the same differences come into evidence as those we have noted in comparing the Ascothoracida with the free living (.attached) forms.

The Rhizocephala are considered by the present day specialists (BROCH 1927, KORSCHELT 1933) to derive from the ectoparasitic Thoracica—(Chelonibia and others). This point of view is founded on the tendency proper to these forms of producing a sort of rootlike processes in their cephalic portion that penetrate into the tissues of the host. According to BROCH (1927) and KORSCHELT (1933) these processes serve to fix the parasite onto host, it is presumably by means of these processes that the additional nutrition of the parasite with the body juices of the host takes place. Subsequently the evolution, according to these authors, has led to the appearance of Rhizocephala in which the penetration into the host's body and the parasite's nutrition at its expense reaches its highest expression. In this group nutrition is exclusively osmotic.

By the above comparisons evidence is obtained that the Ascothoracida differ in various ways from all other suborders of the Cirripedia (sensu stricture). It is especially to be noted that these differences are fairly striking in all larval stages as well as in the adult—if only the latter comparison is possible.

The uniform occurrence of various characteristic features in all Cirripedia s. Str. (Cirripedia excl. Ascothoracica Gruvel). On the one hand and the absence of these same characters in the Ascothoracida on the other (a fact that most clearly stands out when the ways of development in both groups are compared) indicate that the suborder Cirripedia of the present day taxonomics lacks homogeneity. In my opinion it would be apposite to separate it into two groups of equal importance, differing both in the morphology of their larval stages as in the structural plan proper to the adult forms. To one of these groups must be given the designation Cirripedia s. str. with—characteristic for it—cypris-like larvae, a constantly attached mode of life, attachement to the substratum by the cephalic portion, a calcareous skeleton, such as is proper to the free living attached forms, a rudimentary abdomen, localisation of the muscle adductor of valves dorsal to the gut etc. This group includes four of the present day orders of Cirripedia: the Thoracica, Ascothoracica, Rhizocephala and Apoda.

The other group is represented by the Ascothoracida (Ascothoracica Gruvel);

these are primarily predaceous forms capable of freely moving about. They differ herein from the forms constantly attached (to a substratum)—peculiar to which is the ascothoracid larva. In this group no skeletogenous centres are ever formed in the mantle, the adductor muscle lies ventral to the muscle etc. This group is represented by the formerly fifth Cirripedian suborder—Cirripedia Ascothoracica Gruvel. The above enumerated characteristic peculiarities have led me to exclude the Ascothoracida from the Cirripedia s. str. and to give them a place in the system of Entomostraca independent of the Cirripedia (see below). But although the Ascothoracida differ in many essential ways from the Ascothoracica Gruvel owing to which they can not be left in the order Cirripedia (as it is done by the presentday taxonomists) note must be taken of the numerous characteristic features showing the existence of a close relationship between these groups and it is likewise impossible to disregard the circumstance that in most cases the peculiarities in which the Cirripedia differ from the Ascothoracida are of a secondary nature. They must have appeared in the Cirripedia in connection with their going over to an attached mode of life. Whereas the Ascothoracida present—as compared with them—many primitive structural characters.

VOL. 27 1946

## B. A COMPARISON WITH THE COPEPODA.

### a. Adult stages.

The Copepoda and Cirripedia differ from all other orders of Entomostraca by the presence of subimaginal stages in their development. This peculiarity is likewise characteristic for the Ascothoracida. The number of the subimaginal stages varies from one (Cirripedia and Ascothoracida) to several—up to six in Copepoda. The existence of several copepodid larval stages seems to be a subsequently acquired complication of the development cycle. Another character these three groups have in common is the constant number—sixteen at the outmost—of segments and the composition of the body of three distinct portions—the head, thorax and abdomen. The original number of segments is sixteen—of these 5 constitute the cephalic, 6 the thoracic and 5 the abdominal portion. Such is the segmentation in the Calanoidea among the Copepoda, and in the Synagogidae—among the Ascothoracida. In Cirripedia, the abdominal segments having undergone reduction, the total number of segments is from 12 to 13. It is most important to note that in the case of a reduction of segments these changes in all the three groups occur at the expense of the abdominal portion. In Copepoda and in Ascothoracida such a reduction is connected with a parasitic mode of life and in the Cirripedia it is in addition connected with the attached mode of life. The third peculiarity common to all the groups mentioned is the tendency to form a cephalothorax—the tendency to a complete or partial fusion of the first (sometimes of the second also) thoracic segment

with the cephalic portion. Not less characteristic is the presence of a distinct sex dimorphism as expressed in the appearance of dwarf males, the females being parasitic or attached. Further, attention must be drawn to the fact that only in these three Entomostraca groups a distinct parasitism may be observed.

The cephalic portion in Copepoda is normally developed and bears five pairs of appendages; antennules (antennae are absent in the Ascothoracida) and a primitively constructed oral apparatus of the gnawing type. The apparatus includes mandibles, maxillulae and maxillae. The labrum is as a rule but very feebly developed and it is only in certain forms (Siphonostomata) that the oral appendages form a siphon. *No oral pyramid is formed as a rule.*

The thoracic portion is composed of six segments and possess six pair of biramous natatory limbs; of these the anterior ones (the first pair) frequently change into supplementary gnawing stomatopodia. In the Ascothoracida no stomatopodia ever are formed. The abdomen is constituted of five segments and bears a well developed furca—such is also the case in the Ascothoracida. The segments of the cephalic portion are fused together on the dorsal side forming a single carapax. In some forms the first thoracic segment is fused with the head and takes equally part in the formation of the carapax which, in that case, becomes the carapax of the cephalothorax. In the Ascothoracida the same process takes place but their carapax is much more extended and forms a bivalved mantle.

In concluding the analysis of the articulation mention must be made of the role of the antennules in Copepoda. In most pelagic forms the antennules represent a most strong locomotory organ. In the epibenthal Harpacticoida the antennules are frequently modified into grasping organs. These organs are only found in males, they serve to grasp the female during copulation. In such cases the antennules frequently take up the form of shears. In the males of Nannopus palustris Brady, f.i. (Copepoda Harpacticoida) the antennules are composed of six joints (SCHEPHER 1931), like the antennules in the Ascothoracida. This analogy may quite certainly be explained only by convergence the example cited being illustrative of the plasticity of the antennules in the Copepoda. The same may be said of the labrum which in some forms of this order is greatly enlarged and appears as a sheath to the siphon.

The alimentary system in the Copepoda is of simple structure. It is represented by a tubular gut, consisting of fore-, mid- and hind-gut. The gastric diverticula as frontal and fronto-lateral protrusions occur only in semiparasitic forms (Coryceidae and Asterocheiridae) whereas the gut diverticula in the Ascothoracida figure as a characteristic feature.

The nervous system retains the ganglionary structure and tends to highly expressed concentration. The organs of sense are represented by the eyes, and various hairs and additional structures which may occur also on the antennules.



VOL.
27
194

The excretory system in adult forms is represented by maxillary glands. In some instances these glands are of a distinctly nephridical type (Viguirela cauca Maupas) one finds namely a coelomic sac and an excretory duct possessing a funnel (Chappius from Kückenthal and Krumbach 1927, Bd. III). In addition to maxillary glands Achteres possesses maxillipedian glands—the so called "Claus' pulsating organ". In the Ascothoracida only maxillary glands are present. In Calanoida and Pantellidae a slightly developed vascular system may be observed—the heart extends in length over two segments, it has three pairs of ostia. In most Copepoda the vascular system is completely absent, it is characterised by a lacunary system. The Ascothoracida possess only a lacunary system.

### b. Larval stages.

The larval stages are numerous. Some of them (five at the least) are of the nauplius type (ortho- and meta-nauplii)—they are characterized by the presence of a head carapax, by a slight development of the additional structures at its hind end, and an unpaired eye. The Ascothoracida nauplii are very similarly structured, diferring from the Copepoda nauplii by the absence of an unpaired eye. The copepodid larvae exteriorly closely agree with the adult from which they differ in that the earlier stages of development have the same number of segments. The more advanced copepodid larvae have already obtained the full number of segments. It may be concluded from these facts that in Copepoda the subimaginal (as well as the larval) period is more extended at the expense of the increase of the number of larval stages, whereas in the Ascothoracida the opposite tendency may be observed, namely the tendency to a reduction of the larval stages—to an abbreviation of metamorphosis. The initial nauplius stages in this group are frequently in abeyance and of the subimaginal stages a single stage is retained.

The above comparison indicates that the Ascothoracida, although possessing many characters in common with the Copepoda, still may not be included in the order Copepoda, as they differ in the following points: tendency to a strong development of the carapax modified into a bivalvate mantle in which special brood pouches come to be formed: 2) reduction of antennae, 3) formation of an oral pyramid, 4) presence of an adductor muscle of the valves, 5) branching of the gonads and of the gut diverticula within the mantle valves, and 6) only one subimaginal stage.

The characteristic peculiarities common to Copepoda and Ascothoracida are 1) 16 segments of the body, 2) tendency to form a cephalothorax, 3) natatory thoracic limbs and furca, 4) outward (probably also internal) similarity of the nauplii, 5) complete articulation of the well developed abdomen, and 6) similar localisation of the mantle and the germinative apertures in both groups.

TABLE IV (larvae).

| Stages | Characteristic feature | Copepoda | Ascothoracida | Cirripedia | Notes |
|---|---|---|---|---|---|
| Nauplii | Cephalic carapax without frontal spines | + | + | — | The appearance of frontal spines is a secondary phenomenon, it is connected with the development of cephalic glands the spines bearing the openings of these glands |
| | Cephalic carapax with frontal spines | — | — | + | |
| | Unpaired eye | + | — | + | The loss of the unpaired eye observed in the Ascothoracida nauplii must be put in connection with incubation.—This indicates that the rearing of larvae is of ancient origin. |
| | Additional structures at the hind end | ? | — | + | |
| Subimaginal (copepodid, ascothoracid and cypris) stages | Subimaginal stages: one | — | + | + | In Dendrogaster astericola the first—nauplius—larva is enclosed within the egg envelopes of ulterior appearance |
| | several | + | — | — | |
| | Carapax reaching to the half af the body | + | — | — | |
| | Carapax covering the whole body | — | + | + | |
| | Dorsal suture short | — | + | — | Primary |
| | Dorsal suture long | — | + | + | Secondary phenomenon and so is the appearance of a ventral suture—Both must be put in connexion with the development of the cephalic portion |
| | Ventral suture | — | — | + | |
| | Articulation as in the adult | + | + | + | In Copepoda in the late stages |
| | Abdomen composed of from 4 to 5 segment | + | + | — | |
| | Abdomen composed of fewer segments (2 or 3) | — | — | + | |
| | Furca well developed | + | + | — | |
| | Furca rudimentary | — | — | + | |
| | Antennae | + | — | — | The loss of antennae is a secondary phenomenon |
| | Oral pyramid | — | + | + | Of ulterior appearance; developed in connection with the increase in size of the labrum |
| | Mouth appendages of the piercing type | — | + | — | Narrow specialization—the gnawing type is more primitive |



VOL
27
194

TABLE IV (larvae). (Continuation.)

| Stages | Characteristic feature | Copepoda | Ascothoracida | Cirripedia | Notes |
|---|---|---|---|---|---|
| Subimaginal (copepodid, ascothoracid and cypris) stages | Gnawing type | + | — | + | |
| | Thoracopodia biramous, of the natatory type | + | + | + | |
| | Cement glands | — | — | + | Modified dermal glands adaptation to the attached mode of life |
| | Gut branching within the mantle valves | — | + | — | Of secondary appearence |
| | Gut tubular | + | — | + | Primary character |
| | Adductor muscle | — | + | + | Adaptive modification of the maxillary muscle. The muscle sets in movement the valves of the carapax. |
| | Adductor muscle lying dorsally | — | — | + | Secondary character connected with inversion. |
| | Adductor muscle lying ventrally | — | + | — | Primary |
| | Antennules filiform | + | — | — | |
| | Antennules shears-like | — | + | — | Adaptive modifications, appearing in connection with the animal becoming attached to the substratum |
| | Antennules sucker-like | — | — | — | |
| | Skeletal centres | — | — | + | Adaption to the attached mode of life |
| | Inversion at an angle of 90° | — | — | + | |

TABLE V (adult forms).

| Stages | Characteristic feature | Copepoda | Ascothoracida | Cirripedia | Notes |
|---|---|---|---|---|---|
| Imaginal stages (Calanoida Synagogidae, Thoracica) | Cephalic portion normal | + | + | + | Connected with the attached mode of life |
| | Cephalic portion changed to a sole or peduncle | — | — | + | |
| | Antennae | + | — | — | The Reduction of the antennae is a secondary phenomenon |
| | Antennules filiform | + | — | — | |
| | Antennules like shears | — | + | — | |
| | Antennules like rudimentary suckers | — | — | + | |

TABLE V (adult forms). (Continuation.)

| Stages | Characteristic feature | Copepoda | Ascothoracida | Cirripedia | Notes |
|---|---|---|---|---|---|
| Imaginal stages (Calanoida, Synagogidae, Thoracica) | Oral pyramid | — | + | + | Formation of the oral pyramid —a secondary character |
| | Oral appendages of the gnawing type | + | — | + | The gnawing oral appendages are more primitive as compared with those of the piercing type |
| | Oral appendages of the piercing type | — | — | — | |
| | Thoracic limbs of the natatory type | + | + | — | Primitive |
| | Thoracic limbs modified into cirri | — | — | + | Secondary modification connected with the animal having changed to an attached mode of life. |
| | Abdomen not reduced | + | + | — | |
| | Abdomen reduced | — | — | + | —owing to the attached mode of life |
| | Furca of the natatory type | + | + | — | Primitive |
| | Furca rudimentary | — | — | + | Due to the attached mode of life |
| | Carapax covering one half of the body | — | — | + | |
| | Carapax covering the whole body | — | — | + | |
| | The definitive mantle aperture coinsides with the mantle aperture in the larvae | — | + | — | Primary conditions |
| | The definitive mantle aperture corresponding to the hind portion of the mantle aperture in the larva | — | — | + | Secondary modification due to the animal's attaching itself to the substratum with its cephalic portion |
| | Calcareous skeleton | — | — | + | Secondary formation adaptation to the attached mode of life |
| | Calcareous skeleton, aperture lying in the 1 pair of thoracic limbs | — | + | + | |
| | Calcareous skeleton, aperture in the 1 abdominal segment | + | — | — | |
| | The receptacula seminis lie in the thoracic limbs | — | + | — | |

TABLE V (adult forms). (Continuation.)

| Stages | Characteristic feature | Copepoda | Ascothoracida | Cirripedia | Notes |
|---|---|---|---|---|---|
| Imaginal stages (Calanoida, Synagogidae, Thoracica) | Gonads and gut branching within the mantle valves | — | + | — | Secondary |
| | Penis in the 1 abdominal segment | — | + | + | |
| | Attached, non parasitic | — | — | + | Secondary states |
| | Free swimming mobile | + | + | — | Primary state |
| | Parasites | (?) + | + | + | |
| | Primarily dioecious | + | + | + | Primitive conditions |
| | Dwarf males | + (a few) | + | (a few) | A consequence of specialization of the females |
| | Complementary males | — | — | + | |
| | Hermaphroditic | | — | + | Secondary condition connected with the attached mode of life |
| | Adductor muscle of valves situated dorsally | — | — | + | Secondary—due to inversion during metamorphosis |
| | Adductor muscle of valves situated ventrally | — | + | — | Primary condition |
| | The mantle in ♀ contains a special brood pouch | — | + | — | Adaptation, probably of a secondary nature (?) |
| | The young are incubated directly within the mantle cavity | — | — | + | A more primitive condition |

It may be inferred from the above that Copepoda and Ascothoracida are related groups but they stand further away—than the aberrant suborders of the Copepoda from the typical Copepoda forms.

The high specialisation of the recent Copepoda renders a comparison exceedingly difficult, however all three groups have certain structural characters in common indicateng that the Copepoda possess a number of more primitive characters. This fact however does not exclude the existence of a relationship between the three groups and indicates that these three groups are descended from a common ancestor. The following table is illustrative of the above discussed comparative characteristics of the three groups.

It follows from the parallel we have just drawn up that although the Ascothoracida have many characters in common with Copepoda and Cirripedia, they nevertheless can not be put neither in the one nor in the other order named

(VAGIN[1] 1937). In view of this I consider it apposite to make of the Ascothoracida (Cirripedia Ascothoracica Gruvel 1905) an separate order Ascothoracida Wagin 1937 (which genetically is related both to the Copepoda and to the Cirripedia).

*Characteristics of the order.* Entomostraca with bivalvate mantle the enveloping mantle valves are joined together by a short anterodorsal suture and are set in motion by an adductor muscle lying ventral to the gut. Segmentation of the body distinct; number of segments constant (15 to 16) including—5 cephalic, 6 thora- and from 4 to 5 abdominal segments. The cephalic portion bears antennules with shears like claws and an oral pyramid with three pairs of appendages. Antennae are absent in all stages with the exception of the nauplius stages. The thoracic portion bears six pairs of biramous natatory (or uniramous leaf shaped) limbs. The abdominal portion is well developed and possesses a furca at its end. The embryos and larvae develop in special brood pouches—in the mantle of the females. The nauplius and metanauplius stages are according to type but possess no unpaired eye. The ascothoracid (subimaginal) stage resemble the adult forms. It has a bivalvate mantle with a short dorsal suture and a muscle adductor of the valves lying below the gut. The antennules bear shears-like claws, antennae are absent. An oral pyramid containing mouth appendages of the piercing and sucking type is present. Natatory biramous thoracic appendages (5 or 6 pairs). The abdomen is composed of five segments and bears a well developed furca.

In the Ascothoracida the sexes are distinct (Petrarca alone is hermaphroditic). Sexual dimorphism well expressed—dwarf males present. Predaceous, ecto- and endoparasites of Corals and Echinoderms.

## C. THE POSITION IN THE SYSTEM.

The development in the course of evolution of the relations existing between Copopeda, Ascothoracida and Cirripedia may be pictured as follows. Among the Entomostraca forms with a subimaginal stage (VAGIN 1937) and possessing a constant number—not above 16—of segments made their appearance. Owing to these peculiarities the forms mentioned made a group apart in the Entomostraca. Their mode of life must have been pelagic and epibenthal.

The further process of evolution may have gone on in the following manner (VAGIN 1937): on the one hand there is evolution of the forms with a small carapax and the full number of cephalic appendages—from them the present day Copepoda with all their structural peculiarities are derived (fig. 31). On the other hand in forms with a highly developed carapax, no antennae and their antennules changed to grasping organs serving for attachment to the

[1] My name has been erronncously spelt with a V—the right spelling is WAGIN.

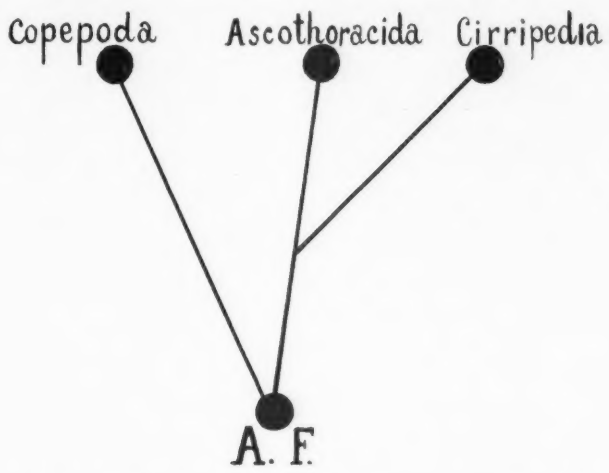



Fig. 31. Diagram of the phylogenetical relations between Copepoda, Ascothoracida and Cirripedia (Explanation in text).

VOL. 27 1946

substractum—evolution went another way. Such organisms were inhabitants of the bottom or the deepest layers of water. Their nourishment consisted of particles of ooze. The oral pyramid must have made its appearance as an adaption, which preserved the oral apparatus from being obstructed when the animal burrowed in the ooze. Later on such forms became adapted to different modes of existence. Some of them came to parasitate (or became semiparasitic) on or in Corals and Echinoderms, and, after various changes, became the present day Ascothoracida. These forms, owing to their narrow specialization came to retain many primitive characters in their organization—a fact which is brought to evidence not only be the study of their embryology, but also by the study of the adult forms (see tables IV and V in the text).

The other direction in evolution is represented by forms that came to be adapted to an attached mode of life—from them the present day Cirripedia originated. In these forms various secondary adaptations made their appearance, namely: a protective calcareous skeleton, cement glands, sucker-like antennules, sac-like mantle, inversion in metamorphosis etc.

The structure of the mantle, of the imaginal appendages, the localisation of the adductor muscle of valves, normally developed (not reduced) abdomen, the primary distinct sexes etc. permit to conclude that the Ascothoracida are of a more primitive structure.

In consequence the Ascothoracida must be put between the Copepoda and Cirripedia as representing an independant order, more closely related to the Cirripedia (fig. 31), than to the Copepoda, which must have diverged from the common ancestral form before the segregation in Ascothoracida and Cirripedia had taken place.

## VII. SUMMARY.

As a result of our investigations it has been possible to establish that 1) Ascothorax ophioctenis Djakonov parasitating in the bursal cavities of Ophiocten sericeum Forb has of all Synagogidae the most complex structure. In the infested Ophiuroid Ascothorax produces swellings of the disc and is the cause of passive castration of the host (indirect destruction of its gonads). The percentage of infested Ophiuroids averages 0.7 % (from 0.02 % to 3.41 %).

Ascothorax inhabits the Kara, the Barents and the Greenland Seas and is a typically arctic form. The females retain a fixed position in the bursa, attached to the bursal walls by means of their shear-like antennular claws. The dwarf males which parasitate together with the female move freely about in the remaining space between the body of the female and the bursal wall. The Ascothorax forms feed on the tissues and the coelomic liquor of the host.

In their morphological structure both males and females of Ascothorax show traces of rudimentation caused by the parasitic mode of life. Owing to the strong development of the ovaries and the brood pouches the mantle in the females expands considerably and becomes nearly spherical. The mantle valves are distinct; they are joined to the body only in the cephalic region, on the dorsal side. In the males the mantle valves are flattened and beanshaped and scarcely cover the body. Both in males and females the body is distinctly segmented, the number of segments amounting to 16. The cephalon bears antennulae composed of five joints and an oral pyramid in which lie three pairs of appendages of the piercing and sucking type (Antennae are absent). The thoracic portion is composed of six segments and bears six pairs of biramous limbs. In the females these limbs are leaf-shaped, presumably in connection with their respiratory function. Dorsally the thorax possesses four pairs of protrusions of which the anterior two serve to support the mantle valves. The abdominal portion is composed of five segments. It is mobile in males, but in females it is fixed and curved like the letter S (an adaptation serving to close the entrance into the brood pouch). The fifth abdominal segment bears well developed furca. In males a small conical penis is disposed on the ventral side of the first abdominal segment. The general plan of structure agrees on the whole with that of the forms previously described: it has, however, been possible to establish a number of new details. Thus antennular nerves and ganglia, the structure of the antennular muscles were described for the first time, these new data proving to be of considerable value from the phylogenetical point of view. A detailed account of the topography of the gut diverticula in males and females (three pairs in the females and two pairs in males) is given. Evidence has been obtained that the so called "testes" or



VOL
27
194

"dermal glands" of other authors found in the thoracopodia of the Lauridae female are the receptacula seminis—a fact recognised by comparing the organs observed in the Ascothorax females with the corresponding organs reproduced in the works of other authors. Aside this the females of Ascothorax were found to possess a glandular organ of unknown function. No duct was found to this "gland". The eggs and larvae develop in the brood pouches from which the larvae issue in their ascothoracid stage (the "cypris" stage of other authors). Basing on various peculiar characteristics such as the feeble development of the cephalon, absence of cement glands, the distinct bivalvate character of the mantle, and many other peculiarities we consider the said larval stage as a special larval type—the *ascothoracid stage*, analagous to the copepoid stage in Copepoda, and the cypris stage (s. str.) in Cirripedia.

2) Evidence was obtained by a comparative analysis of the Ascothoracida that the evolution of this group occurred in two directions.—The one is represented by the development of the Synagogidae and Dendrogasteridae in which a lateral expansion of the mantle takes place and—both in females and in males—the shear-like antennular claws persist showing an increase in function. The dwarf males change to endoparasitism simultaneously with the females. (Synandric forms—with ecto- resp. endobiontic relations between the sexes).

The incubatory period is of longer duration—the larvae leave the female in their ascothoracid stage. These forms are mainly parasites of the Echinoderms.

The other direction in evolution is represented by forms in which a dorso-ventral expansion of the mantle and reduction of the antennulae in females took place (Lauridae). The dwarf males do not become endoparasitic as do the females, they remain ectoparasitic (representing the biological type of athelobiontic forms). The antennules retain their ancestral structure of prochela. The period of incubation is short, the larvae leave the brood pouch of the female in their nauplius stage. As a rule these forms parasitate on and in Corals.

The systematical position of the Petrarcidae is not clear. The most primitive of all the presently existing forms is Synagoga mira. Norm.—a stenothroph predacious Crustacean living in corals (Antipatharia). Owing to its great specialization this form has retained many ancestral structural characters. Basing on this fact as well as on the biology of the Lauridae males it may be concluded that the parasitism on corals is the more ancient and has for its origin the stenotrophic predaceous mode of life.

3) By comparing the Ascothoracida with the Copepoda and Cirripedia it was found that these groups have much in common and must have originated from a common form characterised by oligomeric segmentation, and in the development of which a subimaginal stage had made its appearance. The Copepoda separated from the common ancestor before the segregation in Ascothoracida

and Cirripedia took place. The existence of a closed relation between these two groups may be inferred from the following: the strong development of the carapax, the absence of the antennae, (which were lost before segregation took place), formation of the oral pyramid, and presence of the muscle adductor of valves.

Various differences in the structural plan presented by the adult and larval stages indicate that in Ascothoracida the structure is more primitive than in Cirripedia. The complication of the structure in Cirripedia must be put in connection with these animals going over to an attached mode of life.—In the Cirripedia were developed a calcareous exoskeleton, a muscle adductor of valves lying forward of the valves, inversion in the course of metamorphosis took place, cement glands in the larvae of the cypris stage and a number of other characters made their appearance. On the other hand, in the Ascothoracida, owing to their narrow specialization, a more primitive organisation was retained.

The postembryonic development in Cirripedia closely ressembles the development of the non parasitic attached forms and this permits to infer that the parasitic forms are originated from the attached forms and were not evolved independently.

4) The Ascothoracida are a well developed independent order. They must be taken out of the Cirripedia to which they were consigned as a suborder—Cirripedia Ascothoracida Gruvel 1905, and the now existing order—Cirripedia must be divided in two orders Cirripedia s. str. and Ascothoracica Wagin (1937).

VOL.
27
194

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VOL
27
194

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VOL.
27
1946